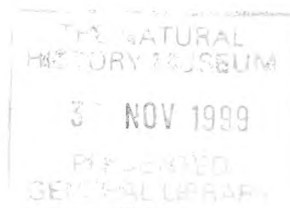


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A new stylophoran echinoderm, *Juliaecarpus milnerorum*, from the late Ordovician Upper Ktaoua Formation of Morocco

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SYNOPSIS. The late Ashgill stylophoran echinoderm *Juliaecarpus milnerorum* gen. et sp. nov. from the Upper Ktaoua Formation of Morocco is characterized by a high degree of thecal symmetry, a large suranal plate and an almost bilaterally symmetrical arrangement of supracentralia on the anterior half of the theca. *Juliaecarpus* was adapted to resting on a soft sea bottom by exploiting the weight-bearing capacity of mud. Locomotion probably occurred through alternating left and right lateral thrusts of the styloid and ossicular spikes against sediment, separated by upward and downward return strokes. In most classifications, *Juliaecarpus* would be placed in the cornutes, owing to the presence of a zygial bar extending from M'_1 to the right posterior part of the thecal frame and to the fact that the marginalia are rod-like and surround several supracentralia and infracentralia. Following recent classifications, however, *Juliaecarpus* is best regarded as an ankyroid, due to its almost bilaterally symmetrical outline, to the possession of styloid processes and to the fact that the posterior zygial plate is a somatic element sutured with the posterior right part of the thecal frame, but not included in the latter. Among ankyroids, *Reticulocarpus hanusi*, *Beryllia miranda* and *Domfrontia pissotensis* most closely resemble *Juliaecarpus*.

INTRODUCTION

The stylophoran controversy

The debated systematic affinities of the stylophorans, a problematic group of marine metazoans of the Palaeozoic covered with an echinoderm-like skeleton of stereomic calcite (Smith, 1980) and variously allied to the echinoderms (e.g. Ubaghs, 1968) or to the chordates (e.g. Jefferies, 1986), have generated great interest in recent years, resulting in the publication of several papers in which their alpha taxonomy as well as their relationships (both within the group and in the context of deuterostome phylogeny) are discussed. Gee (1996) provided updated bibliographical references and a com-

prehensive review of the controversy surrounding these animals. The most recent account of the debate is the scientific correspondence between Peterson (1995) and Jefferies (1997) (but see also Sumrall, 1997 for comments).

Different opinions as to which thecal surfaces and marginal thecal plates are homologous in the two stylophoran groups of the cornutes (Jaekel, 1901) and the mitrates (Jaekel, 1918), as well as disagreement on their anatomical orientation and on the function of their single and jointed exothecal appendage, have led to a proliferation of different and often contrasting morphological terminologies. An additional difficulty is the lack of a standardized plate nomenclature (Caster, 1952; Ubaghs, 1968, 1969, 1981; Jefferies, 1968, 1973, 1981, 1986, 1997; Jefferies & Prokop, 1972; Jefferies & Lewis,

1978; Philip, 1979; Kolata & Jollie, 1982; Kolata *et al.*, 1991; Parsley, 1988, 1991, 1994, 1997, 1998; Ruta, 1998, in press).

Parsley (1997, 1998) and Lefebvre *et al.* (1998) addressed the problematic nature of the stylophorans in a number of papers focussing on their skeletal homologies and interrelationships. In particular, the elegant synthesis by Lefebvre *et al.* (1998) adds to the arguments put forward by earlier authors (e.g. Ubaghs, 1968, 1969, 1981; Parsley, 1988, 1991; Kolata *et al.*, 1991) in support of the homology between the plano-concave thecal surface of the mitrates and the flat thecal surface of the cornutes. Such arguments are based on a detailed comparative morphological study of the following skeletal structures in representatives of both stylophoran groups: 1) the tripartite, jointed exothecal appendage; 2) the apophyses, which project medially from the most anterior pair of marginal thecal plates, M'_1 and M_1 ; 3) the left and right adoral plates, LA and RA, which contribute to the excavation for the insertion of the articulated appendage together with the apophyses; and 4) the zygale/septum complex, which runs obliquely on the flat side of the theca and, at least in its anterior portion, is associated with the same marginal plate (M'_1) in all known stylophorans (see also section on the terminology below).

The constructional and topological similarity of the above-mentioned structures in cornutes and mitrates leads to the unequivocal conclusion that all stylophorans show the same basic anatomical organization (Ubaghs, 1981; Kolata *et al.*, 1991; Peterson, 1995; Parsley, 1997, 1998; Lefebvre *et al.*, 1998), contrary to the opinion expressed by such workers as Jefferies (1986 and references therein), Cripps (1989a) and Cripps & Daley (1994).

The recent discovery of such primitive mitrates as *Vizcainocarpus dentiger* Ruta, 1997 and a morphological comparison between this species and the cornute *Nanocarpus dolambii* Ubaghs, 1991 strengthen the commonly held view that the flat side of the cornute theca corresponds to the plano-concave side of the mitrate theca. However, this view was formerly rejected by me (Ruta, 1997; see also discussion in Ruta, 1998, in press) and I did not compare *Vizcainocarpus* with *Nanocarpus*. In addition, I presented a character-based hypothesis of interrelationships of the mitrocystitid mitrates using several cornute taxa as outgroups, but I neglected most skeletal similarities between cladistically derived cornutes and basal mitrates.

Additional arguments favouring the homology of the flat thecal surfaces in all stylophorans were presented by Ubaghs (1994) in his comparison between the cornute *Lyricocarpus courtessolei* and the mitrate *Chinianocarpus thoralis* Ubaghs, 1961.

After the publication of my 1997 paper on *Vizcainocarpus*, Dr B. Lefebvre (pers. comm.) and Prof R. L. Parsley (pers. comm.) drew my attention to the fundamental resemblance (especially evident in the zygale/septum complex) between the flat thecal surface of *Vizcainocarpus* and that of *Nanocarpus* as well as to the fact that the distinction between cornutes and mitrates, as proposed by those workers who interpret stylophorans as chordates, relies on *ad hoc* hypotheses of character transformation between these two groups (see also below), as previous authors have already pointed out (notably Ubaghs, 1981, Kolata *et al.*, 1991 and Parsley, 1991).

In fact, as noted by Parsley (1997, 1998) and especially Lefebvre *et al.* (1998), the distinction between cornutes and mitrates is no longer valid and ought to be abandoned in favour of the resolution of phylogenetic relationships of all stylophorans as a group. Revisionary work in this field has just begun (Dr B. Lefebvre, pers. comm.; Ms M. Martí-Mus, pers. comm.). In particular, Parsley (1997, 1998) showed that the mitrates, as originally conceived, may not have a common origin after all (i.e. mitrates would be polyphyletic). These results prompt a re-evaluation of current ideas on the evolution and

character distribution of these fossils (however, see below for comments on the results of Parsley's (1997, 1998) analysis).

The stylophoran interpretation adopted

In the present paper, the stylophorans are interpreted as echinoderms, according to the traditional view and contrary to the opinions expressed in some of my earlier works, in which a chordate interpretation was followed and in which the jointed appendage of these animals was regarded as a posterior, locomotory organ, homologous with a chordate tail (references in Ruta, 1998, in press). I now concur with several other researchers that the segmented appendage of cornutes and mitrates, henceforth referred to as the aulacophore (Ubaghs, 1968), is primarily an anterior feeding organ of ambulacral origin, although, as Sumrall (1997: 269) pointed out, the resemblance between the aulacophore and the ambulacrum '... does not allow for the falsification of the hypothesis that [these two structures] are homologous'.

The interpretation of the aulacophore as an echinoderm arm fully satisfies criteria of morphological similarity. Thus, for Lefebvre *et al.* (1998: 104) the aulacophore '... may be homologous to a single crinoid arm'. However, this view has been emphatically rejected by some authors, notably Jefferies (1986) and Gee (1996). The arguments in support of the echinoderm affinities of the stylophorans are thoroughly discussed by Ubaghs (1968, 1981), Parsley (1988, 1991, 1994, 1997, 1998) and Lefebvre *et al.* (1998) and will not be repeated in this paper.

Unlike Ubaghs (1981) and in partial agreement with other authors, I also regard the aulacophore as a locomotory device which may have functioned in different ways in different stylophorans (e.g. Jefferies & Prokop, 1972; Kolata & Jollie, 1982; Jefferies, 1984, 1986; Parsley, 1988, 1991; Cripps, 1989a; Kolata *et al.*, 1991; Daley, 1992; Woods & Jefferies, 1992; Ruta & Bartels, 1998).

A third interpretation of the aulacophore, considered only as a locomotory device but not homologous with a chordate tail, was discussed by Philip (1979), Kolata & Jollie (1982) and Kolata *et al.* (1991) (synthesis in Jefferies, 1986 and Ruta, 1998, in press).

The calcichordate theory of Jefferies and co-workers (see especially Jefferies, 1986) deserves a final, brief comment. It represents a thorough elaboration of Gislén's (1930) hypothesis that the ancestry of the vertebrates is rooted into the extinct assemblage of the 'carpod echinoderms', encompassing today the groups solutes, cornutes, mitrates, cinctans and ctenocystoids, and was dealt with at length by Gee (1996). According to the calcichordate theory, most solutes (see Daley, 1996) and all cornutes are seen as stem-group chordates, all mitrates as stem-group members of the three modern chordate subphyla, Tunicata, Acraniata and Craniata, and cinctans and ctenocystoids as stem-group echinoderms.

As far as the stylophorans (cornutes and mitrates) are concerned, the calcichordate theory requires radical internal and external anatomical changes in passing from the cornutes to the mitrates, notably the loss of the mid and distal portion of the cornute aulacophore and a re-organization of the remaining, proximal portion into the very similar tripartite structure observed in the mitrates. Ubaghs (1981), Parsley (1991) and Lefebvre *et al.* (1998) emphasized the difficulties associated with the anatomical modifications demanded by Jefferies' theory. Such modifications are supported by dubious or, more often, no fossil evidence at all. Thus, as Lefebvre *et al.* (1998: 104) put it, acceptance of Jefferies' (1986) arguments implies that '... the median and distal parts of the aulacophore suddenly disappeared in the cornutes to reappear exactly identical but upside-down in mitrates'.

Despite my own initial convictions (references in Ruta, 1998, in

press), I now remain very sceptical when it comes to a consideration of the fossil evidence favouring the calcichordate interpretation of the stylophorans. Such an interpretation discounts obvious morphological and topological similarities between the anatomical organization of cornutes and that of mitrates and makes poorly supported or unsubstantiated claims as to the morphological changes which occurred at the cornute-mitrate transition (summary in Jefferies, 1986 and Cripps, 1989a).

The wealth of morphological data produced by Jefferies and co-workers is impressive. However, the morphological comparative analysis of the relevant fossils poses certain problems, especially as far as the anatomical evidence in support of the transition from cornutes to mitrates is concerned. The theory is, therefore, rejected in favour of widely accepted and well-corroborated views on skeletal homologies in the stylophorans.

Terminology

Morphological nomenclature, plate notation and anatomical orientation of the stylophorans are those proposed by Ubaghs (1968) in the *Treatise on Invertebrate Paleontology* (see also Ubaghs, 1969) and adopted by subsequent workers (e.g. Parsley, 1988, 1991, 1994, 1997, 1998, Sumrall *et al.*, 1997, Lefebvre *et al.*, 1998, etc.). The identification of the marginal plates in the new stylophoran described here is based on a recent character analysis by Parsley (1997, 1998) and on a comparative study of morphological data gleaned from various sources, especially Ubaghs (1968, 1969), Jefferies & Prokop (1972), Cripps (1989a), Cripps & Daley (1994) and Lefebvre *et al.* (1998).

A list of the morphological terms applied to the stylophorans and a detailed description of their external and internal anatomical organization were provided by Ubaghs (1968). I emphasize the fact that, in most cases, such a terminology does not imply anatomical or functional interpretations of the observed structures. As stated by Ubaghs (1968), the interpretations are often entirely conjectural (see, however, Jefferies, 1986 and discussion in Ruta, 1998, in press).

The most frequently cited morphological terms used in the anatomical description (Fig. 1) are briefly explained below and appear in bold in this section of the paper only. Most of them apply to all stylophorans, a few are restricted to the vast majority of these fossils and some are introduced here in conjunction with the description of the new taxon.

A stylophoran is divided morphologically into a posterior **theca** and an anterior **aulacophore**, the latter representing an arm (i.e. a feeding organ of ambulacral origin extending beyond the oral surface; see Sumrall, 1997). The convex and flat surfaces of the theca consist of a **dorsal integument** and a **ventral integument** respectively. The main thecal opening, at the opposite end of the theca with respect to the aulacophore insertion, is the **anus**. The **main axis**, or **longitudinal axis** of the body, is the intersection between the plane of bilateral symmetry of the aulacophore and the plane of flattening of the theca. The **oro-anal axis** runs from the centre of the aulacophore insertion to the anus. **Proximal** and **distal** indicate the position of a structure close to or away from the junction between the theca and the aulacophore. **Median**, **admedian** and **lateral** (or **marginal**) indicate the position of thecal structures (e.g. integument plates) with respect to the longitudinal axis.

The theca is framed by **marginal plates**, or **marginalia**, surrounding several **central plates**, or **centralia**, termed **supracentralia** and **infracentralia** on the dorsal and ventral surfaces respectively. The marginalia are labelled antero-posteriorly (i.e. from the thecal excavation for the aulacophore insertion to the anus) as M'_1, M'_2, M'_3, \dots , etc. on the left side, and as M_1, M_2, M_3, \dots , etc. on the right side

of the theca. Each marginal plate consists of a **dorso-lateral projection**, sloping laterally and ventrally, and a **ventral projection**. The two projections meet at the lateral margins of the theca. The two anterior supracentral plates articulated with M'_1 and M_1 and contributing to the excavation for the aulacophore insertion are the left and right **adoral plates**, or **adoralia** (LA and RA respectively).

A large, flexibly articulated plate (perhaps an enlarged supracentral element) present between the rearmost ends of the thecal margins and roofing over the anal opening in the new stylophoran described here is termed the **suranal plate**, or **suranal**.

The **zygal bar**, or **zygal** (apparently absent in such cornute genera as *Ceratocystis* Jaekel, 1901 and, perhaps, also *Nevadaecystis* Ubaghs, 1968 and *Protocystites* Hicks, 1872; see also Ubaghs, 1963, 1967, 1987, Jefferies, 1969, 1986 and Jefferies *et al.*, 1987), is a strut-like bar connecting M'_1 with the posterior part of the right margin of the theca on the ventral surface and is homologous with the septum of mitrates (Ubaghs, 1968, 1969; Kolata & Jollie, 1982; Kolata *et al.*, 1991; Parsley, 1991, 1997, 1998; Lefebvre *et al.*, 1998). In several stylophorans, such as the new form described in this work, the zygal consists of a **posterior zygal plate** (a somatic element sutured with the right posterior part of the thecal frame but not included in the latter) and a **posterior process** of M'_1 .

The proximal part of the aulacophore usually consists of **tetramerous rings**, each composed of a pair of dorsal plates, termed the **tectals**, and a pair of ventral plates, or **inferolaterals**. The robust ventral element present in the intermediate part of the aulacophore is the **styloid** or **stylocone**. The term styloid is preferred over stylocone when the structure in question bears well-developed projections (spikes, cusps, blades, etc.), as in mitrates and in several mitrate-like cornutes (Jaekel, 1918; Parsley, 1991, 1997, 1998; Lefebvre *et al.*, 1998). However, the distinction between stylocone and styloid has no morphological basis, as correctly pointed out by Ubaghs (1968, 1981), for these terms refer to the same (homologous) skeletal element in all stylophorans. Such a distinction was adopted by Jefferies (1986) who denied the homology between the cornute stylocone and the mitrate styloid (but see rebuttal by Lefebvre *et al.*, 1998), as explained above.

Each segment of the distal part of the aulacophore consists of a ventral **ossicle** articulated with a dorsal pair of **cover plates**. The structures visible on the internal surface of the aulacophore ossicles and those present on the dorsal (internal with respect to the inside of the theca) surface of the most anterior portions of M'_1 and M_1 will be discussed separately in the descriptive anatomical section of this paper.

AIMS OF THE STUDY

Background

In the collections of the Department of Palaeontology, The Natural History Museum, London, there is abundant material of a new stylophoran echinoderm from upper Ashgill mudstones in Morocco, collected in the early 1990s. Several features of its dorsal and ventral integuments, thecal frame and aulacophore justify its attribution to a new genus and species, although it is similar in several respects to such mitrate-like cornutes as *Reticulocarpos hanusi* Jefferies & Prokop, 1972, *Domfrontia pissotensis* Chauvel & Nion, 1977) and *Beryllia miranda* Cripps & Daley, 1994 (see section on morphological comparisons below).

In traditional classifications of the stylophorans (e.g. Ubaghs, 1968), the fossils described herein would be assigned to the cornutes, because it possesses a zygal bar extending from plate M'_1 to the right

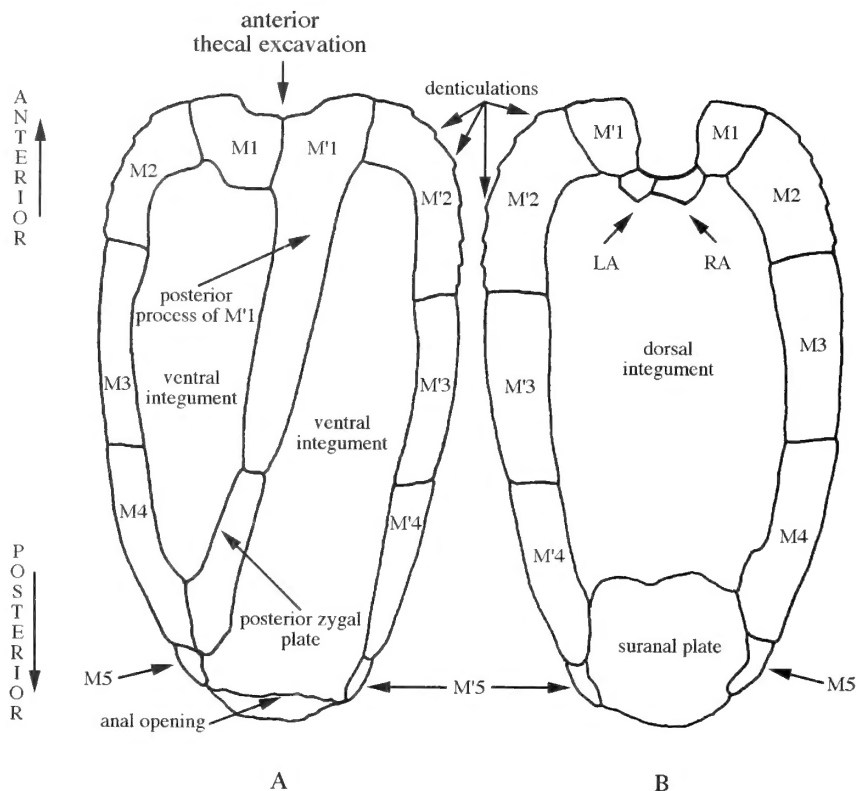


Fig. 1 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Schematic reconstruction showing orientation, anatomical nomenclature and plate terminology of the theca. **A**, ventral aspect. **B**, dorsal aspect.

posterior part of the thecal frame, because its marginal plates are elongate and rod-like and because its dorsal and ventral integuments consist of a relatively large number of plates. In Parsley's (1997, 1998) recent phylogenetic analysis, the above-mentioned taxa to which the new Moroccan form bears close resemblance, several other almost bilaterally symmetrical and mitrate-like cornutes and all the mitrates are set apart from the strongly asymmetrical (and often boot-shaped) cornutes and are given a rank of their own, for which Parsley (1997, 1998) proposed the name Ankyroida. The new Moroccan taxon would be an ankyroid according to Parsley's (1997, 1998) phylogenetic scheme.

The order Ankyroida comprises stylophorans in which the thecal outline approaches bilateral symmetry in varying degrees, the posterior zygial plate is usually a separate somatic element (i.e. this plate is not part of the marginal frame of the theca) and the styloid bears projections in the form of spikes, cusps or blades. However, stylophorans other than the ankyroids form a paraphyletic assemblage in Parsley's (1997, 1998) phylogeny. Parsley (1997, 1998) retained the former name Cornuta as emended by Ubahgs (1968) for this assemblage (not characterizable in the light of shared derived features), but suppressed the Mitrata.

The present study aims to: 1) reconstruct and describe a late Ordovician Moroccan ankyroid; 2) discuss its morphology from a functional viewpoint, with emphasis placed on the stability of the animal in water currents and on the feeding and locomotory roles of its aulacophore; 3) compare it with several other Ordovician ankyroids.

The discovery of the new Moroccan taxon prompts a reassessment

of stylophoran interrelationships as well as a critical analysis of the cornute-mitrate transition (Cripps, 1989a, b, 1991; Daley, 1992; Cripps & Daley, 1994) in the light of more traditional views on homologous skeletal characters in these echinoderms. Such arguments will be developed in another paper.

Material and methods

Most specimens are preserved as incomplete, slightly to heavily disrupted external moulds of the theca and aulacophore. Incomplete internal moulds of isolated thecal elements (especially marginalia) and, more rarely, of almost complete thecae have also been recorded. In very few individuals, the thecae are fully articulated and the degree of disruption affects mainly the alignment of the left and right marginalia. The dorsal integument is usually completely preserved, both externally and, more rarely, internally. The ventral integument, on the other hand, is invariably poorly preserved, heavily disrupted or missing and the boundaries between the infracentralia are difficult to observe. The posterior end of the theca is generally disrupted.

The zygial bar is often found broken, but in some individuals, both the posterior zygial plate and the posterior process of M'_1 are uncrushed and their relative size and proportions with respect to the rest of the theca can be accurately reconstructed. The loss of supracentralia in few specimens allows the dorsal surface of the zygial bar (and especially its suture with the thecal frame) to be observed. Sometimes, compaction of the fossils resulted in the squashing of the supracentralia against the zygial bar, thus reproducing the boundaries of the latter and the nature of the contact of the distal end of the

posterior zygial plate with the posterior part of the right thecal margin. Numerous isolated marginal elements reveal details of their stereom texture and the degree of curvature of their internal surfaces (i.e. the surfaces oriented towards the internal side of the theca).

Rarely is the aulacophore found in place. Its proximal part, when preserved, is invariably incomplete or crushed. Its intermediate and distal parts are sometimes found articulated with each other and slightly disrupted. More often, only disarticulated styloids, cover plates and ossicles are found.

The fine matrix in which the skeletal moulds occur reproduces changes in the stereom texture of various skeletal elements, both externally and internally. In some cases, the external surface of the specimens appears to be heavily weathered and covered with a network of criss-crossed cracks, often obliterating almost completely both plate boundaries and skeletal fabric.

The fossil material required little mechanical preparation. Some specimens were dissected with a needle to partially expose the appendage and the peripheral margins of the thecal frame. Almost all specimens were cast with black-stained latex. Latex peels were coated with ammonium chloride sublimate and photographed at a low angle of illumination to emphasize details of the external skeletal surface (see also Ruta & Bartels, 1998).

The reconstruction of the external aspect of the animal and of several details of its external and internal anatomy (e.g. suranal plate, apophyses, internal surface of M'_1 , peripheral flange, styloid, ossicles, etc.) are based on camera lucida sketches drawn to scale and on a series of engineering projections in dorsal, ventral, lateral, anterior and posterior views (Fig. 2A–E). The engineering drawings were based on morphological information gleaned mainly from the following specimens (see also list of the material examined below): BMNH EE 3069a, b, 3070a, b, 3072a, b, 3101a, b, 3115a, b, 3119a, b, 3127a, b, 3144a, b, 3163, 3178a, b. The cross-section of the marginalia was reconstructed from the latex peels by cutting these with a razor blade at different levels perpendicular to the direction of maximum elongation of each marginal plate. Observations were carried out using a Nikon SMZ–10 binocular microscope.

SYSTEMATIC PALAEOLOGY

Phylum **ECHINODERMATA** Fleming, 1828
Class **STYLOPHORA** Gill & Caster, 1960
Order **ANKYROIDA** Parsley, 1997
Family unassigned

REMARKS. As conceived by Parsley (1997, 1998), the order Ankyroida includes the former order Mitrata Jaekel, 1918 and some representatives of the former order Cornuta Jaekel, 1901, the latter almost universally considered as a paraphyletic group by stylophoran workers (e.g. Jefferies, 1986; Cripps, 1991; Daley, 1992; Woods & Jefferies, 1992; Cripps & Daley, 1994; Parsley, 1997, 1998; Lefebvre *et al.*, 1998). Although I am confident about the monophyly of the Ankyroida, I shall not elaborate upon the interrelationships between representatives of this group. These ought to be reassessed after the inclusion of several recently described taxa in a new, expanded character matrix for all known stylophorans.

I have not included a family in the systematic palaeontology section above. In this, I follow some systematists' view that traditional systematic categories ought to be abandoned (e.g. see discussion in Craske & Jefferies, 1989) and that hierarchically clustered clades within a monophyletic group do not need naming. This approach avoids the introduction of additional names in the

systematic literature and eliminates ambiguities resulting from continuous redefinitions of previously established taxonomic names. A rankless phylogenetic scheme is especially desirable in the case of extinct groups (such as stylophorans) with a very discontinuous fossil record, because the discovery of additional taxa and/or characters is likely to affect taxon relationships and character distribution to a considerable extent.

Because very few subgroups within the stylophorans can be shown to be monophyletic (see discussion in Ruta, 1998, in press), a subdivision of the whole class into taxonomic ranks seems to be inadvisable at present (but see also Caster, 1952 and Ubaghs, 1968, 1969). Current taxonomic subdivisions, especially for the cornutes (Cripps, 1991; Daley, 1992; Cripps & Daley, 1994), ought to be reconsidered. The major problem with them is the fact that they have been generated by character coding built upon assumptions of character transformation at the cornute-mitrate transition (Lefebvre *et al.*, 1998). Assumption-laden choice of some characters, based on theory and process, also characterized a recently published data set of mine (Ruta, 1997).

The results of other phylogenetic analyses of the stylophorans as a group or of different subsets of them differ significantly. Thus, there is need for an integration of the various data sets and for a critical evaluation of the characters used.

In their monograph on Middle Ordovician cornutes from Normandy, Cripps & Daley (1994: 107) erected the family Reticulocarpidae, for which they provided the following diagnosis: 'The Reticulocarpidae are cornutes with optic embayments, slit-like terminal mouths, no branchial skeleton and ventral spikes on the mid- and hind-tail ossicles'. As I shall explain in detail below, the stylophoran described in the present work is extremely similar to the genus *Reticulocarpus*.

However, in the light of Parsley's (1997, 1998) cladistic analysis and of the various problems associated with Cripps' (1991) and Cripps & Daley's (1994) character coding, I question the sister group relationship between *Reticulocarpus hanusi* Jefferies & Prokop, 1972 and *Beryllia miranda* Cripps & Daley, 1994, grouped together in the Reticulocarpidae by Cripps & Daley (1994).

I am more inclined to accept Parsley's (1997, 1998) conclusion that *Reticulocarpus* and *Prokopicystis mergli* Cripps, 1989a are each other's closest relatives and that, together, they form the sister group of the genus *Hanusia* Cripps, 1989b (see also section on morphological comparisons below).

Parsley's (1997, 1998) data matrix likewise presents some problems (e.g. presence of some redundant characters, poorly defined states, low number of characters, wrong coding for certain features in some stylophoran taxa, etc.). Despite this, a preliminary parsimony analysis of Parsley's (1997, 1998) data matrix using PAUP version 3.1.1 (Swofford, 1993) (with inclusion of modified coding for several of his chosen characters, exclusion of redundant characters and corrections of several wrongly coded characters) produced results similar to those of his original run (the latter was based on reweighting of characters) and preserves in part the original tree structure. These results will be extensively discussed in a separate publication in conjunction with a revision of stylophoran interrelationships.

Genus *JULIAECARPUS* nov.

TYPE SPECIES. *Juliaecarpus milnerorum* sp. nov.; late Ashgill (late Rawtheyan), Upper Ktaoua Formation, Morocco. The only known species.

DERIVATION OF NAME. After Julia J. Day (Department of Biology,

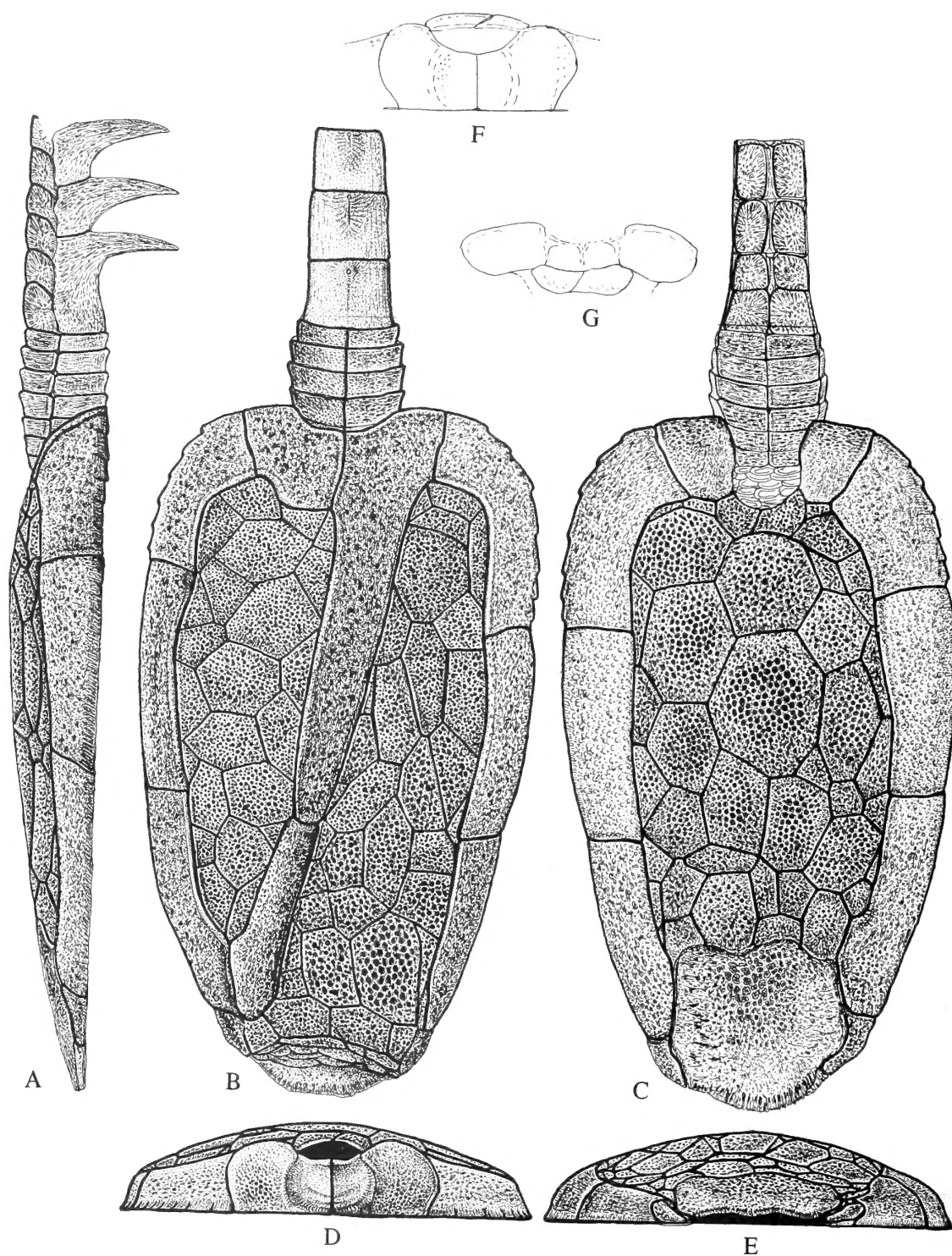


Fig. 2 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of external aspect. **A**, right lateral view of theca and aulacophore. **B**, ventral view of theca and aulacophore. **C**, dorsal view of theca and aulacophore. **D**, anterior view of theca (aulacophore removed). **E**, posterior view of theca. **F**, schematic aspect of anterior thecal excavation showing apophyses and adoralia. **G**, schematic reconstruction of most anterior part of dorsal thecal surface showing adoralia and dorso-lateral projections of M'_1 and M_1 . Arrangement of integument plates, cover plates, tectals and inferolaterals is hypothetical.

University College, London), for her constant encouragement and for providing much useful advice. The suffix *-carpus* is a latinized version of the Greek word *καρπος* (carpos), fruit, gender masculine.

DIAGNOSIS. An ankyroid stylophoran echinoderm characterized by: extreme reduction in size of M'_5 and M_5 ; absence of dorsal bar between M'_1 and M_1 ; posterior zygial plate almost straight and with slightly expanded and flattened distal half; poorly pronounced denticulations present on lateral margins of M'_2 and M_2 ; nearly bilaterally symmetrical arrangement of subpolygonal supracentralia on anterior half of dorsal integument; occurrence of a large suranal plate of irregular and variable shape flexibly articulated with M'_4 , M_4 , M'_5 and M_5 .

***Juliaecarpus milnerorum* sp. nov.** Figs 1–8, Pls 1–8

DERIVATION OF NAME. After Drs Andrew R. Milner (Department of Biology, Birkbeck College, University of London) and Angela C. Milner (Department of Palaeontology, The Natural History Museum, London), for their continuous support and exchange of ideas with the author over the years.

HOLOTYPE. The Natural History Museum, London: Department of Palaeontology, BMNH EE 3070a, b.

PARATYPES. The Natural History Museum, London: Department of Palaeontology, BMNH EE 3069a, b, 3071–2a, b, 3073–4, 3075a, b, 3079a, 3080–1a, b, 3083a, 3084–6, 3088–9, 3090, 3093–4, 3095a, b, 3098, 3101–4a, b, 3105, 3108–9a, b, 3111, 3113, 3114a, b, 3115a, b, 3116a, b, 3117, 3121–2, 3123a–c, 3124–5a, b, 3127a, b, 3129a, b, 3131–2a, b, 3134–7a, b, 3138–9, 3140–1a, b, 3143, 3144–7a, b, 3149a, 3150a, b, 3152a, b, 3153, 3155a, b, 3157, 3158a, b, 3160a, b, 3161, 3162a, b, 3163–4, 3166–7a, b, 3168a–c, 3169, 3170, 3171a, b, 3173a–c, 3175a, b, 3176–7, 3178a, b, 3180–1, 3183–4a, b.

DIAGNOSIS. As for the genus.

LOCALITY. Specimens were collected from locality 756 of Destombes (see also Chauvel, 1971), about 7 km west-south-west of Tazzarine, near Tiz n'Takhrir, Morocco. The reference map is Tazzarine Sheet of 1:100,000 topographical survey. The map coordinates are: x = 477,75; y = 417.

HORIZON. The fossil material occurs in light grey mudstones in the Upper Ktaoua Formation, which lies at the base of the southern part of the Ktaoua plain in the Moroccan Anti-Atlas. The formation consists mainly of grey-green arenaceous argillites interspersed with rare bands of oolitic iron or phosphatic nodules and varies in thickness from 70 m to 110 m.

Fossils are mainly concentrated in three different levels: a first level situated 30 m above the base of the formation and dominated by trinucleid and phacopid trilobites; a second level situated 10 m above the previous level and containing a trinucleid fauna; a third level encompassing the upper two-thirds of the formation, where a rare but well preserved and diverse fauna (more abundant than in the previous two levels) is recorded in widespread pelitic carbonate lenses.

The fauna of the Upper Ktaoua Formation includes, among the other taxa, several brachiopods (e.g. *Eostropheodonta intermedia*, *Eochonetes canaliferus*, *Chonetoida radiatula*, *Comatopoma sororium*) and trilobites (e.g. *Baniaspis globosa*, *Brongniartella platynota marocana*, *Dreyfussina struvei*, *Eudolaites maiderensis*, *Flexicalymene ouzregui*, *Klouceka poueytoi*, *Lichas marocanus*, *Mucronaspis greti*, *M. termieri*, *Actinopeltis* sp., *Amphitryon* sp., *Calymenella* sp., *Dionide* sp., *Onnia* sp., *Selenopeltis* sp., *Stenopareia* sp.), some echinoderms (e.g. *Destombesia diedra acuta*, *Echino-*

sphaerites aurantium transversalis, *Heliocrinites ouguerfensis*, *Maghreboecystis pachythea cupuliformis*, *M. p. robusta*, 'Placocystites' *bohemicus*), rare conulariids, cephalopods, gastropods, bivalves, ostracods and abundant microplankton.

Juliaecarpus milnerorum (henceforth referred to as *Juliaecarpus* for brevity) comes from the third level.

AGE. Although most fossils in the Upper Ktaoua Formation are endemic, the fauna shows affinities with late Ashgill elements from the British Isles, Bohemia, Poland and Sweden. In particular, species belonging to certain genera of brachiopods (e.g. *Eostropheodonta*) and trilobites (e.g. *Brongniartella*, *Flexicalymene* and *Mucronaspis*) are extremely similar to congeneric species found in upper Ashgill rocks of northern, central and eastern Europe.

Destombes *et al.* (1985) suggested that the trinucleid trilobites (e.g. representatives of the genus *Onnia*) indicate an upper Rawtheyan age for the upper part of the Upper Ktaoua Formation, where *Juliaecarpus* occurs. Detailed palaeobiogeographical comparisons between late Ordovician faunas from different regions of the Mediterranean Province can be found in Destombes *et al.* (1985), Destombes & Willefert (1988) and Havlíček (1990).

With regards to *Juliaecarpus*, this stylophoran is very similar to several middle Ordovician and some late Ordovician ankyroids from France and Bohemia (e.g. the genera *Reticulocarpus*, *Beryllia* and *Domfrontia*; see also section on morphological comparisons below). Discoveries of other stylophorans from Morocco (e.g. Chauvel, 1971; Cripps, 1990; Beisswenger, 1994) strengthen the affinities between Ordovician North African faunistic elements and coeval fossil faunas from several European regions (see also Chauvel, 1981, 1986).

OTHER REFERRED MATERIAL. Chauvel (1971: 56, fig. 3f) briefly described a poorly preserved specimen of a stylophoran from the Upper Ktaoua Formation (Destombes Collection, no. 756c), provisionally referred by him to the family Kirkocystidae Caster, 1952 (formerly placed in the lagynocystid mitrates, but now generally referred to the peltocystid mitrates; Jefferies, 1973; Kolata *et al.*, 1991; Parsley, 1991). The specimen in question is the internal mould of a lower thecal surface displaying a considerable degree of disruption. Unfortunately, Chauvel's (1971) description was not accompanied by photographs and it is, therefore, difficult to ascertain the affinities of this fossil. Chauvel (1971) regarded it as an undetermined genus and labelled it as AVII.

Based on his line drawings, however, AVII may belong to *Juliaecarpus*. This is suggested by the relative proportions of the preserved marginalia, including the plate referred to by Chauvel (1971) as the posterior process, based on his attribution of the specimen to the kirkocystids. The plate in question may alternatively be interpreted as a posteriorly displaced posterior zygial plate. The relative size and proportions of the posterior process of M'_1 with respect to the preserved marginalia are very similar to those observed in *Juliaecarpus*.

ANATOMICAL DESCRIPTION

Theca

GENERAL ASPECT (Figs 1, 2). The theca of *Juliaecarpus* consists of 10 marginal plates (or marginalia) forming a peripheral frame interrupted posteriorly at the level of the anal opening and showing an anterior excavation for the insertion of the aulacophore. The theca approaches a high degree of bilateral symmetry and is longer than wide, subelliptical to vaguely pyriform in outline and with a length/

width ratio of about 1.72. The maximum thecal width is at about two-fifths of the way posteriorly along the oro-anal axis.

A comparison between the maximum thecal sizes reported by Cripps & Daley (1994) in several solutes, cornutes and mitrates and the thecal sizes of some of the most complete and least disrupted specimens of *Juliaecarpus* shows that the latter ranks among the smallest stylophorans recorded to date. Estimated thecal length values in the best preserved specimens range between 7 mm and 10 mm, whereas thecal width values in the same specimens are comprised between 4 mm and 6 mm (see also Table 1). As discussed below, morphological variation, both in the general thecal proportions and in the shape and size of the individual plates, is small.

The lateral thecal margins are only slightly convex for most of their length, subparallel or gently diverging in their anterior half, slightly converging posteriorly and merging smoothly into the antero-lateral, lobe-like angles of the theca. These are blunt and shaped approximately like an arc of about 90° in plan view. The left margin of the theca is slightly longer than the right margin, which suggests that the anal opening may have faced slightly rightward in life (see also Cripps & Daley, 1994). As a result of this difference in length, the oro-anal axis is not aligned with the longitudinal axis of the aulacophore, but is displaced slightly to the right of the latter.

A dorsal and a ventral integument, each composed of several polygonal plates of different shapes and sizes, are attached to the medial margins of the dorso-lateral and ventral projections of the marginalia. A large, irregularly polygonal supracentral element, the suranal plate, roofs over the anal opening and is interposed between the rearmost parts of the lateral thecal margins.

The boundaries of the anal opening could not be observed directly in any of the specimens examined, due to the extreme dorso-ventral flattening of the theca in its posterior third, to the generally poor preservation of the rearmost infracentralia and to the fact that the suranal plate is often found collapsed onto the internal side of the ventral thecal surface.

In some individuals, however, both the dorsal and the ventral thecal surfaces are preserved more or less fully articulated and a morphological comparison between part and counterpart suggests that the suranal plate either extended slightly beyond the posterior margin of the ventral integument or corresponded in position with the latter (see also description below). Thus, the anal opening faced either slightly ventralward or posteriorly in life and, as in most other ankyroids, was almost certainly slit-like, although the reconstruction of its outline is only tentative.

In longitudinal section, the theca of *Juliaecarpus* is shaped approximately like a hydrofoil (see also discussion on the morpho-functional adaptations of the theca in relation to the stability of the animal in water currents). The dorsal integument is likely to have been smoothly convex in lateral view and to have reached its maximum curvature at a point situated presumably slightly anterior to its central part. It probably sloped gently rearward and ventralward in life, as suggested by the fact that the height of the marginalia decreases uniformly antero-posteriorly, being about twice greater at the level of the anterior thecal excavation than at the level of the anus.

Transverse sections of the theca at various levels along the longitudinal axis of the aulacophore are probably not very dissimilar in

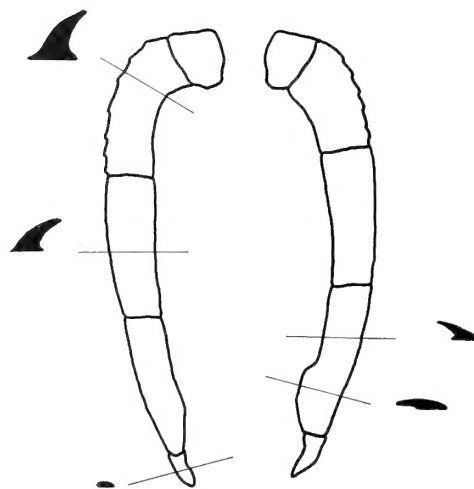


Fig. 3 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Cross-section of the marginalia at different levels along the thecal frame.

outline. Major morphological differences are due to the different curvature and width of the dorso-lateral projections of the marginalia, both of which decrease antero-posteriorly (Fig. 3).

VARIATION. Morphological differences between the most complete specimens of *Juliaecarpus* (see Table 1) as well as between isolated, homologous skeletal elements of its theca (especially marginalia, notably M'_1) are negligible. Ontogenetic variation (if any) could not be detected, since the most complete individuals differ little in size and, therefore, their ontogenetic ages are assumed to be approximately the same.

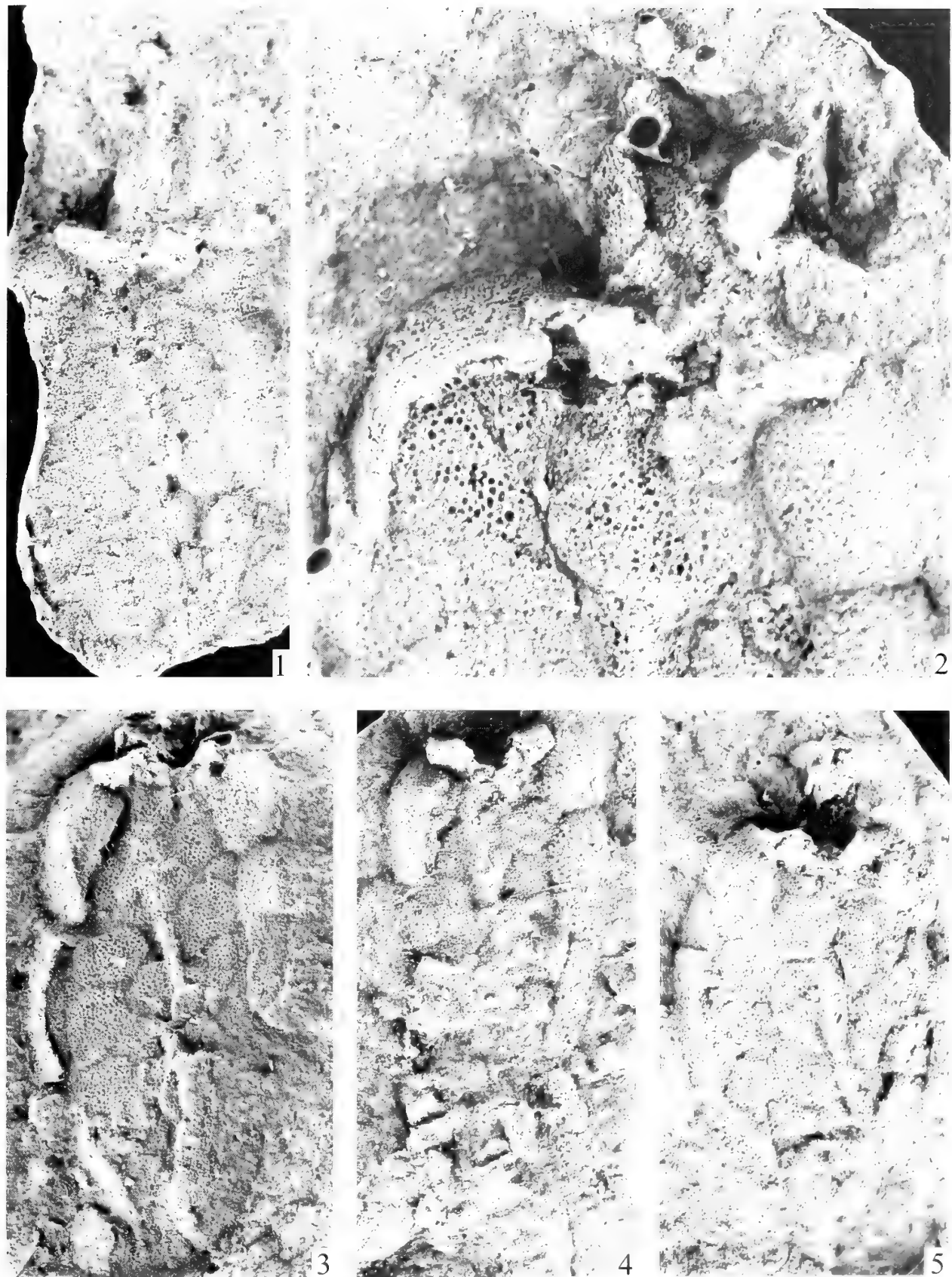
Table 1 Estimated maximum thecal widths and lengths in some individuals of *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco.

Specimen	Thecal length	Thecal width
BMNH EE 3069	10	6
BMNH EE 3070	7	4
BMNH EE 3072	9.5	5.5
BMNH EE 3083	9	5
BMNH EE 3101	10	5.5
BMNH EE 3119	7.5	4.5
BMNH EE 3121	10	6

Differences can be observed in the general outline of the theca (i.e. in its length/width ratio and in the degree of divergence of the lateral margins from the oro-anal axis in a posterior direction), in the curvature of M'_2 and M_2 in plan view, in the shape and curvature of the posterior zygial process of M'_1 and of the posterior zygial plate, in the shape and arrangement of the supracentralia, in the more or less

PLATE 1

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3101, $\times 9$; poorly preserved dorsal aspect of theca, aulacophore and obliquely oriented zygial bar. 2, EE 3072, $\times 20$; arrangement of supracentralia on anterior half of theca and slightly disrupted aulacophore. 3, EE 3144, $\times 10$; almost complete dorsal aspect of theca, arrangement of supracentralia and obliquely oriented zygial bar. 4, EE 3077, $\times 8$; poorly preserved theca in dorsal aspect with well preserved aulacophore insertion. 5, EE 3119, $\times 10$; well preserved theca in dorsal aspect showing almost undisrupted arrangement of supracentralia and suranal plate.



pronounced development of the peripheral flange and of the lateral thecal denticulations (both of which are normally reduced in size) and in the outline and relative size of the suranal plate.

Disruption and, occasionally, slight deformation of the fossil material are partially responsible for the observed variations of the thecal shape.

MARGINAL PLATES. The marginalia are divided into a group of five plates on the right side and a group of five plates on the left side of the theca. The rearmost left and right marginalia, M'_5 and M_5 , are scarcely visible, due to the generally poor preservation of the posterior part of the theca (see below).

The marginalia which occupy the same position in the left and right series with respect to the aulacophore insertion are not mirror images of each other. Rather, they show small but consistent differences in length and, to a much lesser extent, in shape. Each of the marginalia consists of a wider, dorso-lateral projection and a narrower, ventral projection. In cross-section, the dorso-lateral projections narrow slightly antero-posteriorly along the thecal frame and appear to be slightly wider than, and up to twice as wide as, the ventral projections, depending upon the position of the plate in the left or right marginal series. Conversely, the ventral projections are of almost uniform width throughout the left and the right series (e.g. Pl. 1, figs 3–5; Pl. 2, figs 1–5; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5). The dorso-lateral projections (Fig. 3) are gently to strongly convex in cross-section and slope ventralward and laterally, whereas the ventral projections are always flat. The convexity of the dorso-lateral projections is slightly more accentuated at the level of the antero-lateral angles of the theca and decreases rapidly in antero-posterior direction, so that at the level of its postero-lateral angles, the projections become almost flat (Pl. 1, figs 1–5; Pl. 2, figs 2, 4–5; Pl. 5, figs 1–2, 4; Pl. 7, figs 2, 4–6). The dorso-lateral and ventral projections of the marginalia meet at an acute angle forming a sharp lateral margin. Such an angle varies from about 30° in the most posterior portions of the thecal frame to about 70° at the level of its antero-lateral angles.

The thecal margins show a poorly developed flange (e.g. Pl. 1, figs 2–5; Pl. 2, figs 4–5; Pl. 7, fig. 2) characterized by a fibrillar stereom and restricted to the anterior half of the thecal frame.

The most anterior marginal plates, M'_1 and M_1 , contribute to the anterior thecal excavation for the aulacophore insertion (described in the next section). The space through which the internal cavity of the aulacophore communicates with the inside of the theca is roofed over by two adoral plates (see below) and delimited ventrally by the apophyses of M'_1 and M_1 . Given the complicated morphology of the internal (thecal) surface of M'_1 and M_1 and the fact that M'_1 contributes to the zygial bar through its posterior process, both plates (including those parts of them which are visible from the outside in dorsal view, notably their dorso-lateral projections) will be described in detail in conjunction with the description of the internal aspect of the theca.

The asymmetries observed in the thecal frame are mainly due to the unequal size of M'_2 and M_2 , the length of the latter being approximately $4/5$ the length of the former. Both plates are strongly curved medially in plan view and contribute to the lateral half of the right and left antero-lateral angles of the theca. Their dorso-lateral

projections are wider than those of more posterior marginalia. The dorso-lateral projection of M_2 is of approximately constant width throughout the length of the plate and is slightly wider than the posterior half of the dorso-lateral projection of M'_2 . The lateral margins of both plates bear poorly pronounced serrations with a gently sloping anterior surface and a steeply sloping posterior surface (Pl. 1, figs 2–4; Pl. 2, figs 1, 3, 5; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5; Pl. 5, figs 1–3; Pl. 7, fig. 2). The serrations result from the intersection of the lateral margins of M'_2 and M_2 with faint, transverse undulations visible on the lateral third of the dorso-lateral projections of these plates. The undulations become progressively shallower dorsalward before disappearing gradually. The serrations decrease slightly in size antero-posteriorly and disappear immediately posterior to the sutures between M'_2 and M'_3 and between M_2 and M_3 . The ventral projections of M'_3 and M_3 are of almost constant width, but widen slightly near their anterior ends and show characteristic embayments along their medial margins, marking a sudden change in their curvature (e.g. Pl. 2, fig. 1; Pl. 3, figs 1–5; Pl. 4, figs 1–2, 4–5).

M'_3 and M_3 are shaped like elongate rods and are of approximately equal shape and size. Both plates are only gently convex laterally, their dorso-lateral projections show slightly concave to gently sinuous medial margins and their width decreases slowly antero-posteriorly. Their ventral projections possess broadly concave medial margins and are slightly narrower than their dorso-lateral projections. The medial margin of the ventral projection of M_3 is often divided into a straight to gently concave posterior half and a more deeply concave anterior half (e.g. Pl. 2, fig. 1; Pl. 3, figs 1–2, 4; Pl. 4, figs 2–4).

M'_4 and M_4 resemble M'_3 and M_3 in their elongate and rod-like aspect, but while M_4 is either slightly shorter than or equal in length to M'_3 , M'_4 is always shorter than M'_3 . Their dorsolateral projections are slightly narrower than those of more anterior marginalia throughout most of their length, but their posterior ends are expanded medially (especially in M_4) to contact the suranal plate (see below). The lateral margins of M'_4 and M_4 are very gently convex. The ventral projection of M_4 widens posteriorly sending a broadly triangular, medial spatulate flange in contact with the rearmost part of the posterior plate of the zygial bar along an antero-posteriorly elongate, straight suture. The flange forms a continuum with a similar, medially projected, subhorizontal and subrectangular flange of the dorso-lateral projection of M_4 , thus interrupting posteriorly the trough-like internal surface of the plate (e.g. Pl. 1, figs 4–5; Pl. 2, figs 2–5; Pl. 5, fig. 2; Pl. 7, fig. 2; Pl. 8, fig. 3). The posterior ends of both M'_4 and M_4 are blunt, although their poor preservation does not permit their accurate reconstruction.

In some specimens, two small and irregular skeletal fragments with a characteristic reticulate stereom texture flank the suranal plate and are apparently loosely attached to the posterior ends of M'_4 and M_4 from which they are distinguished by the smaller width of their anterior half (e.g. Pl. 1, figs 4–5; Pl. 2, figs 2, 4; Pl. 7, figs 2, 4–5; Pl. 8, fig. 3). These fragments are interpreted as extremely reduced plates M'_5 and M_5 , loosely juxtaposed to the posterior half of the lateral margins of the suranal plate (see below). In some individuals (e.g. Pl. 2, fig. 4), the medial margins of M'_5 and M_5 seem to be slightly

PLATE 2

Juliacarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. 1, EE 3079, $\times 8$; incomplete theca in ventral aspect with poorly preserved infracentralia. 2, EE 3129, $\times 8$; almost complete theca in dorsal aspect with disrupted supracentralia. 3, EE 3129, $\times 8$; poorly preserved theca and aulacophore in ventral aspect, with faint impression of zygial bar and poorly preserved suranal plate. 4, EE 3178, $\times 20$; posterior half of theca in dorsal aspect, with well preserved suranal plate and posterior zygial plate in contact with right posterior part of thecal frame. 5, EE 3072, $\times 9$; almost complete but posteriorly disrupted theca in dorsal aspect.



bent towards the oro-anal axis and possess a blunt, rounded or plectrum-shaped posterior margin. In other specimens (e.g. Pl. 1, figs 4–5; Pl. 7, figs 2, 4–5), M'_5 and M_5 are vaguely rectangular or sub-semielliptical.

ANTERIOR THECAL EXCAVATION. The anterior thecal excavation occupies less than one quarter of the maximum thecal width and is formed mainly by the medially directed apophyses of M'_1 and M_1 and, in part, by the left and right adoralia (see below). The apophyses (Figs 2F, 6; Pl. 6, figs 1–3) are irregularly semielliptical to semicircular in outline and gently excavated both longitudinally and transversely. A shallow groove runs almost parallel to the dorsal margin of the upper half of each of the two apophyses, thus delimiting a smaller dorsal region from a slightly larger ventral region. A poorly defined, low ridge runs from the mid point of the medial margin of the apophysis to its centre just below the shallow groove. The ridge separates a deeper, medio-dorsal subtriangular area from a shallower, latero-ventral area.

The surface of each of the two apophyses slopes slightly forward near its ventral margin, but its upper half is almost vertical. Laterally, the apophyses merge smoothly into the ventral half of the dorso-lateral projections of M'_1 and M_1 (see description below) from which they are separated by a poorly pronounced, medially concave, crescent-shaped, blunt lateral margin.

ADORALIA. The left and right adoralia, LA and RA, occupy the most anterior part of the dorsal integument and roof over the anterior thecal excavation. Their preservation is invariably poor in the specimens examined and their margins are usually difficult to discern. In plan view, they are sometimes visible immediately posterior to the anterior thecal excavation (Fig. 2F–G; Pl. 1, figs 2–5; Pl. 2, figs 2, 5; Pl. 7, fig. 2). They are slightly smaller than the surrounding dorsal integument plates and RA is slightly larger than LA. Both plates vary in shape and size in different individuals, but this variation may be the result of disruption, at least in part. The presence of a right adoral orifice (a small opening piercing or notching RA; Ubaghs, 1968) cannot be detected. Despite the poor preservation, a median adoral is almost certainly absent.

Antero-laterally, each of the two adoralia is sutured with a triangular facet sitting on the antero-medial part of a wedge-like structure originating from the medial half of the dorso-lateral projections of M'_1 and M_1 (see description of these plates below).

LA is irregularly quadrangular to subpentagonal, slightly wider posteriorly than anteriorly and about half to two-thirds as large as RA. RA is usually longer than wide and subrectangular to subtrapezoidal in outline, generally with a broadly convex postero-lateral margin and with a gently concave medial margin accommodating LA.

Both adoralia possess a gently convex to flat dorsal surface. Partial collapse of these elements as a result of burial resulted in their lying slightly lower with respect to the dorsal margins of the dorso-lateral projections of M'_1 and M_1 . In life, LA and RA probably formed a gently arcuate structure bridging the space between the dorsal, antero-medial facets of M'_1 and M_1 , thus sitting immediately above the apophyses. The space comprised between the adoralia and the

apophyses was probably spindle-shaped to irregularly elliptical in life.

ZYGAL. The zygial (or zygial bar) runs obliquely from the left antero-lateral angle of the theca to the postero-lateral fourth of the right part of the thecal frame and is formed by a robust, posterior process of plate M'_1 and by a posterior, elongate plate sutured with M_4 and, perhaps, M_5 . The ventral surface of the zygial is flat, whereas its dorsal surface is very gently convex and with a poorly pronounced subcentral keel (see below).

The length of the posterior zygial plate is about 5/7 the length of the posterior process of M'_1 . The plate is at an angle of about 30° with the oro-anal axis and either forms a wide, obtuse angle with the M'_1 process or is aligned with it. Its left and right margins are almost straight and diverge slightly antero-posteriorly. The average width of the plate is comparable with or slightly greater than that of the ventral projections of the marginalia. The posterior third of the plate is vaguely rectangular and spatulate and its left margin contacts the posterior end of M_4 along a gently arcuate, longitudinal suture (Pl. 1, figs 1, 3–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 1, 5; Pl. 4, fig. 1). The posterior margin of the posterior zygial plate is poorly preserved in the material observed and cannot be reconstructed with accuracy. It might have contacted the antero-medial angle of M_5 , assuming the correct identification of this element (see above).

The process of M'_1 (Pl. 1, figs 1–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 1–2, 5; Pl. 4, figs 1, 5; Pl. 5, fig. 2; Pl. 6, figs 1–3; Pl. 7, figs 2–4; Pl. 8, fig. 3) is straight or, rarely, gently bent in its posterior half and lies slightly to the left of the oro-anal axis for most of its length, forming an angle of about 20°–25° with such an axis. The process is wider than the ventral projections of the marginalia, especially in its anterior two-thirds, and is about half as wide at its posterior end as at the level of the suture between M'_1 and M_1 . The lateral margins of the zygial process converge slightly posteriorly.

DORSAL INTEGUMENT. The supracentralia are mostly irregularly polygonal and sutured with each other along straight margins. Rarely they show gently curved margins. Some supracentralia, especially those situated along or in proximity to the oro-anal axis, are generally as wide as, or slightly wider than, the dorso-lateral projections of the marginalia. The supracentralia differ in shape and size, but most of them are roughly hexagonal or pentagonal. Rarely is their outline triangular or quadrangular. In at least one specimen (Pl. 3, fig. 4), the ventral surface of the dorsal integument is clearly visible.

Although no apparent distribution pattern is observed, the median and admedian supracentralia are on average larger than those sutured with the medial margins of the thecal frame. Generally, two subhexagonal supracentralia are distinguished from the others by their larger size and by the fact that they occupy a median position on the posterior half of the dorsal integument. Sometimes, a left and a right longitudinal row of three slightly smaller and subpentagonal plates flank the two subhexagonal supracentralia. Some of the supracentralia lying along the medial margins of the thecal frame are much longer than wide. The supracentralia which occupy the posterior half of the dorsal integument are usually of irregular shape and

PLATE 3

Juliacarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3070, × 9; almost complete ventral aspect of theca with slightly disrupted zygial bar; note styloid in right lateral view and poorly preserved ossicles. **2**, EE 3144, × 10; incomplete ventral aspect of theca with disrupted zygial bar. **3**, EE 3101, × 9; poorly preserved ventral aspect of theca, with almost complete proximal aulacophore, well preserved styloid and proximal ossicles. **4**, EE 3121, × 8; internal aspect of dorsal side of theca, heavily disrupted along the posterior half of its right margin; note the internal, trough-like aspect of the marginalia. **5**, EE 3072, × 9; almost complete ventral aspect of theca; note robust posterior zygial plate.



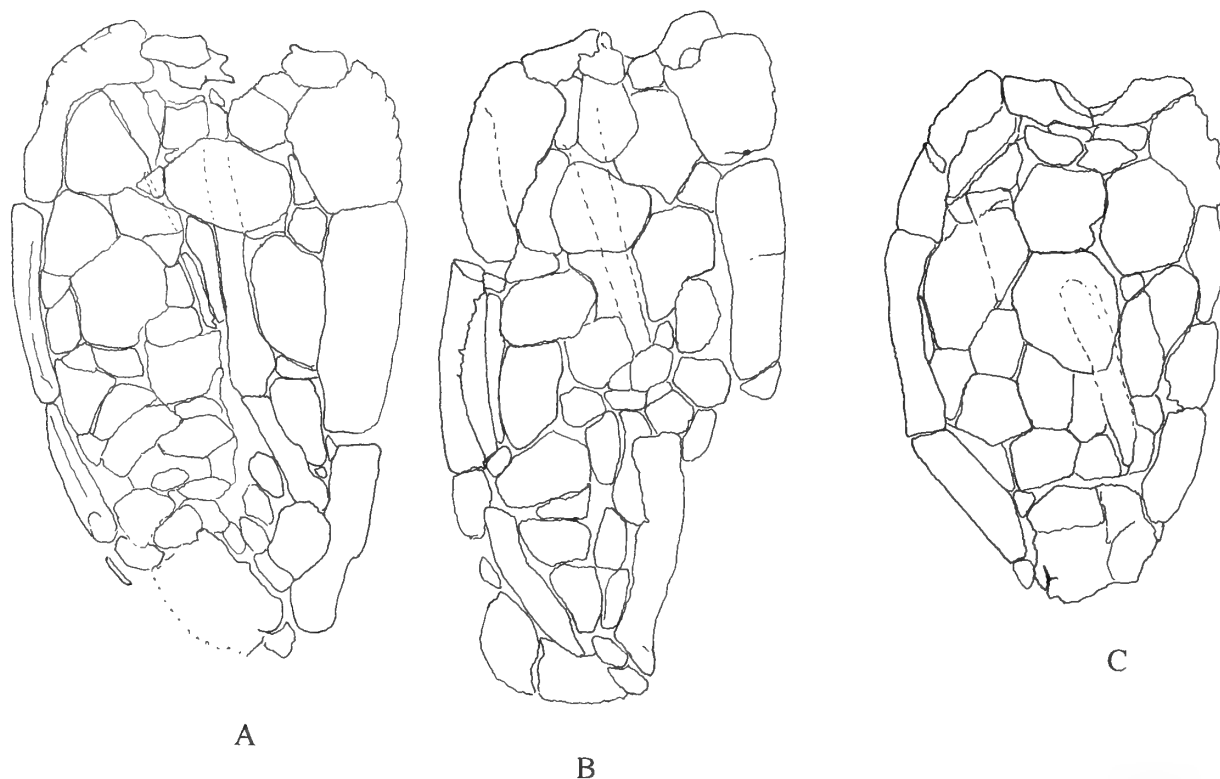


Fig. 4 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Camera lucida sketches of outline of supracentralia in different individuals. **A**, EE 3072, $\times 6$. **B**, EE 3144, $\times 7$. **C**, EE 3119, $\times 7$.

subequal size (Fig. 4; Pl. 1, figs 2–5; Pl. 2, figs 2, 4–5; Pl. 3, figs 2, 4; Pl. 5, figs 1–2; Pl. 7, fig. 2, 4–5; Pl. 8, fig. 3).

A large suranal plate (Figs 1–2, 5; Pl. 1, fig. 5; Pl. 2, figs 4–5, 4; Pl. 3, fig. 4; Pl. 4, fig. 5; Pl. 5, figs 1–2; Pl. 7, figs 2, 4; Pl. 8, fig. 3), sloping slightly ventralward towards its posterior margin, is present between the rearmost margins of M'_4 and M_4 . Its posterior margin roofs over the anal opening. In some specimens, the suranal is broadly trapezoidal in outline. In others, it is rectangular or, rarely, roughly elliptical. Although the suranal is variable in shape, it is always possible to distinguish four margins: a straight to gently sinuous anterior margin loosely articulated with a variable number of posterior supracentralia; two irregularly sinuous lateral margins in contact along their posterior half with the medial margins of M'_5 and M_5 and along their anterior half with the rearmost part of the medial margins of M'_4 and M_4 ; and a broadly convex, posterior margin with a variable degree of curvature and usually displaying a well developed fringe (see description of stereom below). The posterior margin is usually very slightly offset with respect to the position of the oro-anal axis. The dorsal surface of the suranal plate is flat to very gently

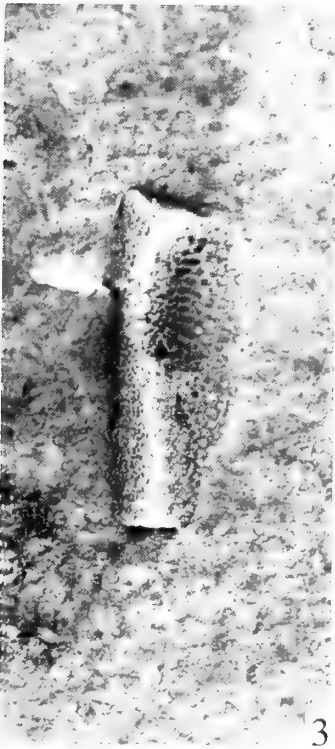
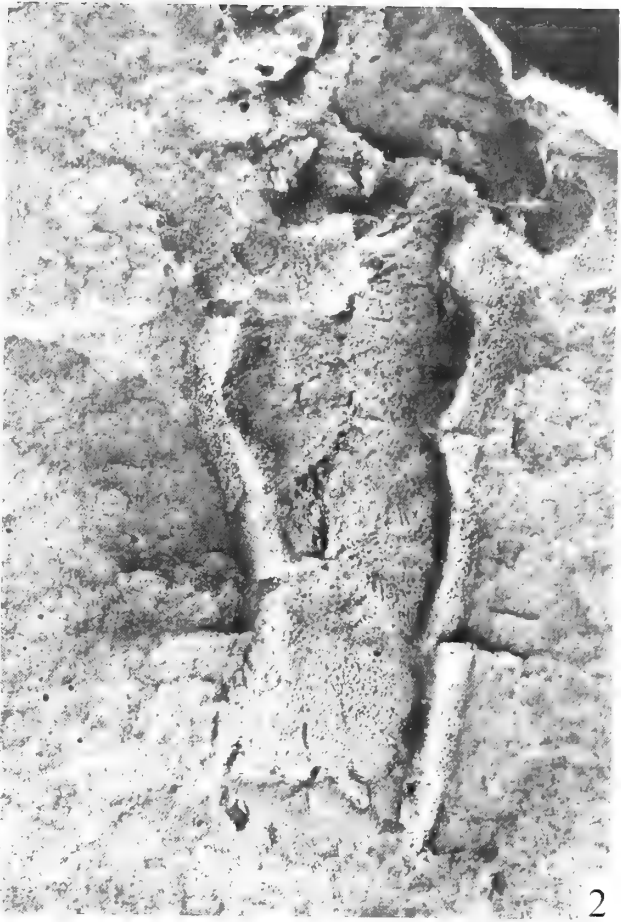
convex in its central part and flat along its posterior margin and slopes gently ventralward near its lateral margins.

VENTRAL INTEGUMENT. The ventral integument (Pl. 2, figs 1, 3; Pl. 3, figs 1, 3, 5; Pl. 4, figs 1–2, 4) is flat and divided by the zygial bar into two antero-posteriorly elongate areas of slightly different size, the left area being slightly broader than the right area. The infracentralia are generally more poorly preserved than the supracentralia, but seem to have been more irregular in outline and of various shapes and sizes. As in the case of the supracentralia, they do not seem to have been imbricated or to have shown a regular arrangement, but their boundaries are difficult to delimit.

Unfortunately, in none of the specimens of *Juliaecarpus* is the ventral integument complete and its posterior part is invariably damaged or missing. Therefore, the reconstruction of the infracentralia which floor the anal opening is only tentative and it is impossible to say whether the ventral margin of the anus was bordered by flexibly articulated, narrow, elongate platelets arranged in a fan-like pattern (as in the case of the ankyroid *Amygdalotheca*

PLATE 4

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3069, $\times 10$; heavily disrupted theca in ventral aspect; note shape and proportions of posterior zygial process. **2**, EE 3115, $\times 10$; incomplete and laterally compressed theca in ventral aspect. **3**, EE 3181, $\times 15$; isolated marginal element in internal view, possibly M_4 . **4**, EE 3162, $\times 10$; incomplete and disrupted theca in ventral aspect. **5**, EE 3162, $\times 10$; posteriorly disrupted theca in dorsal aspect with partially preserved supracentralia.



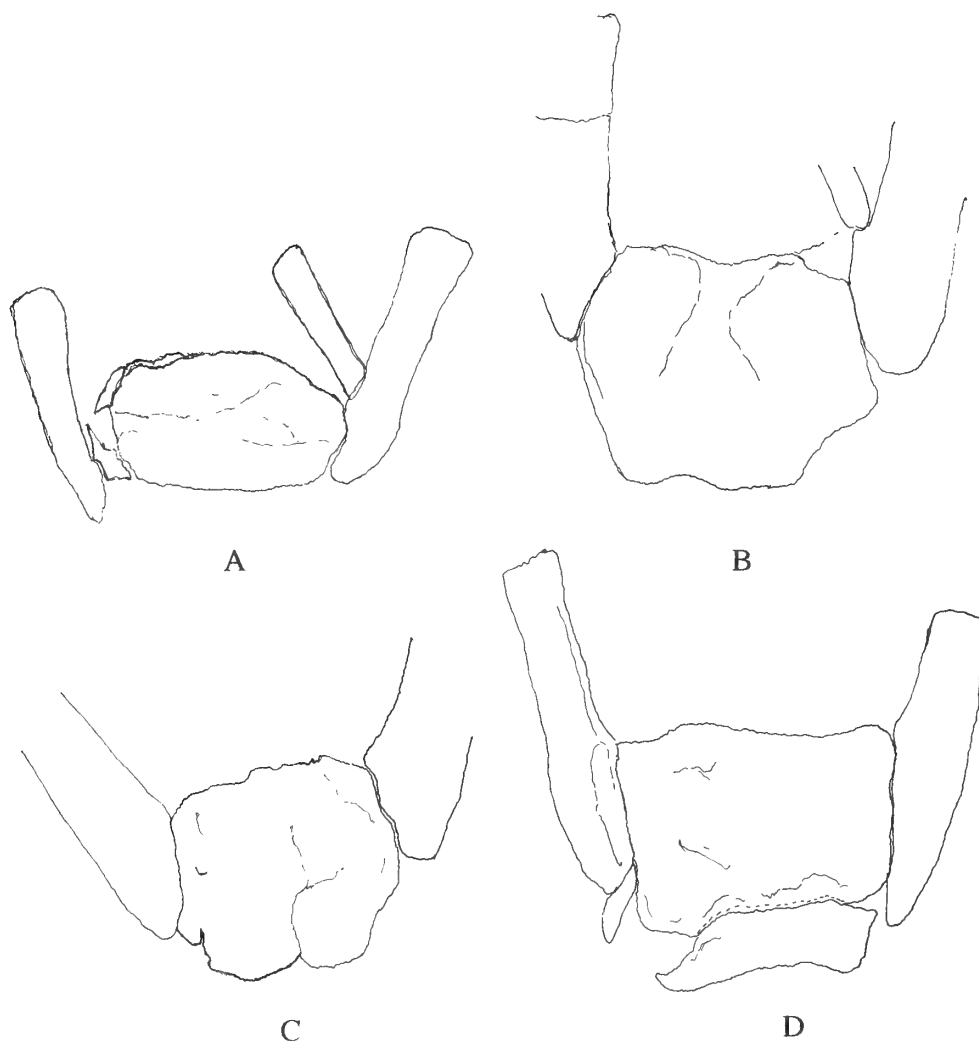


Fig. 5 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Camera lucida sketches of outline of suranal plate in different individuals. **A**, EE 3184, $\times 7.5$. **B**, EE 3178, $\times 13$. **C**, EE 3119, $\times 13$. **D**, EE 3121, $\times 7.5$ (seen from the inside).

griffei Ubaghs, 1969) or by a mosaic of relatively large, polygonal elements (as in *Reticulocarpus hanusi* Jefferies & Prokop, 1972).

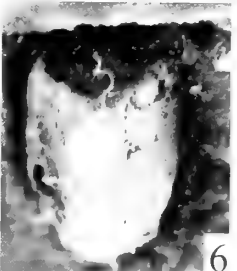
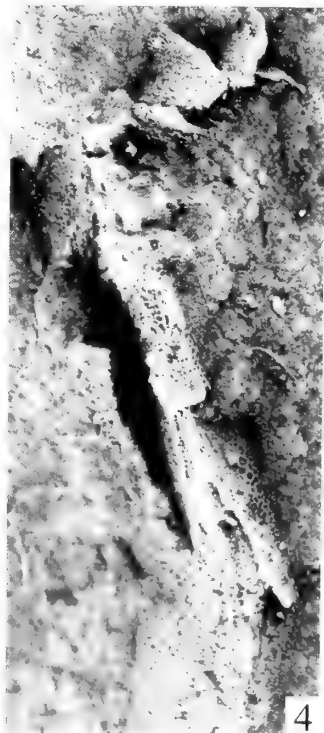
INTERNAL ASPECT OF THE THECA. The internal surfaces of both the supracentralia and the infracentralia are featureless. The surface of the marginalia facing towards the inside of the theca is trough-like (Fig. 3; Pl. 3, figs 1–5; Pl. 4, figs 1–4). Its cross-section does not show abrupt changes in curvature, but it varies considerably in depth depending upon the relative width of the dorso-lateral and ventral projections of the marginalia. Thus, at the level of the antero-lateral angles of the theca, the surface is approximately semiparabolic to semicircular in cross-section, whereas halfway along the length of

the lateral thecal margins, its section is semielliptical. It becomes shallower and broadly hyperbolic at the level of the postero-lateral angles of the theca.

The internal surfaces of plates M'_1 and M_1 and of the zygial bar show a complex morphology. In fully articulated specimens of *Juliaecarpus*, the dorso-lateral projections of M'_1 and M_1 are largely visible in dorsal view. They contribute laterally to the medial parts of the antero-lateral angles of the theca and project medially into the apophyses for the aulacophore insertion (see above). M'_1 and M_1 do not differ remarkably from each other except for the presence of a posteriorly directed process contributing to the zygial bar in M'_1 . In what follows, therefore, I shall

PLATE 5

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3115, $\times 10$; laterally compressed and disrupted theca in dorsal aspect, with displaced supracentralia and poorly preserved styloid and ossicles. **2**, EE 3069, $\times 10$; almost complete theca in dorsal aspect, with slightly displaced marginalia and supracentralia; note disrupted plates of proximal aulacophore. **3**, EE 3071, $\times 15$; isolated proximal aulacophore plates, ossicles, cover plates and proximal-most portion of theca in dorsal aspect. **4**, EE 3098, $\times 10$; poorly preserved marginalia and styloid articulated with first ossicle in left lateral view. **5**, EE 3157, $\times 15$; isolated plate M_2 in dorsal aspect. **6**, EE 3151, $\times 15$; poorly preserved styloid with broken anterior spike in ventral aspect.



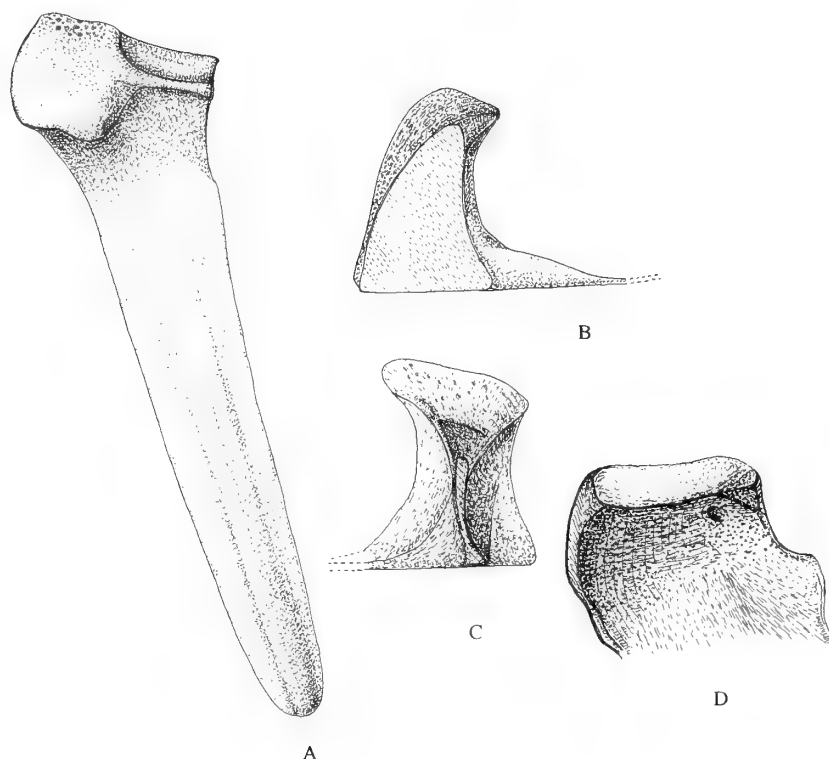


Fig. 6 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of plate M'_1 and of its zygial process. **A**, dorsal aspect. **B**, left lateral aspect of most anterior part. **C**, right lateral aspect of most anterior part. **D**, internal aspect of most anterior part (rear end of plate slightly tilted dorsally).

describe in detail only the internal surface of M'_1 including its zygial process (Fig. 6).

In ventral view, the boundary between M'_1 and its posterior process corresponds to a hypothetical, oblique line connecting the posterior end of the suture between M'_1 and M_1 with the posterior end of the suture between M'_1 and M'_2 . On the internal surface of M'_1 , this line delimits the posterior boundary of a flat, subrectangular region sloping slightly dorsalward both anteriorly and medio-laterally. The anterior boundary of this region is represented by a poorly pronounced crest with a broadly concave dorsal margin. Such a crest forms the dorso-medial margin of the left apophysis. It becomes less pronounced and flatter laterally, where it widens to form a blunt-topped, crescentic ridge separating the apophysis from the dorso-lateral projection of M'_1 .

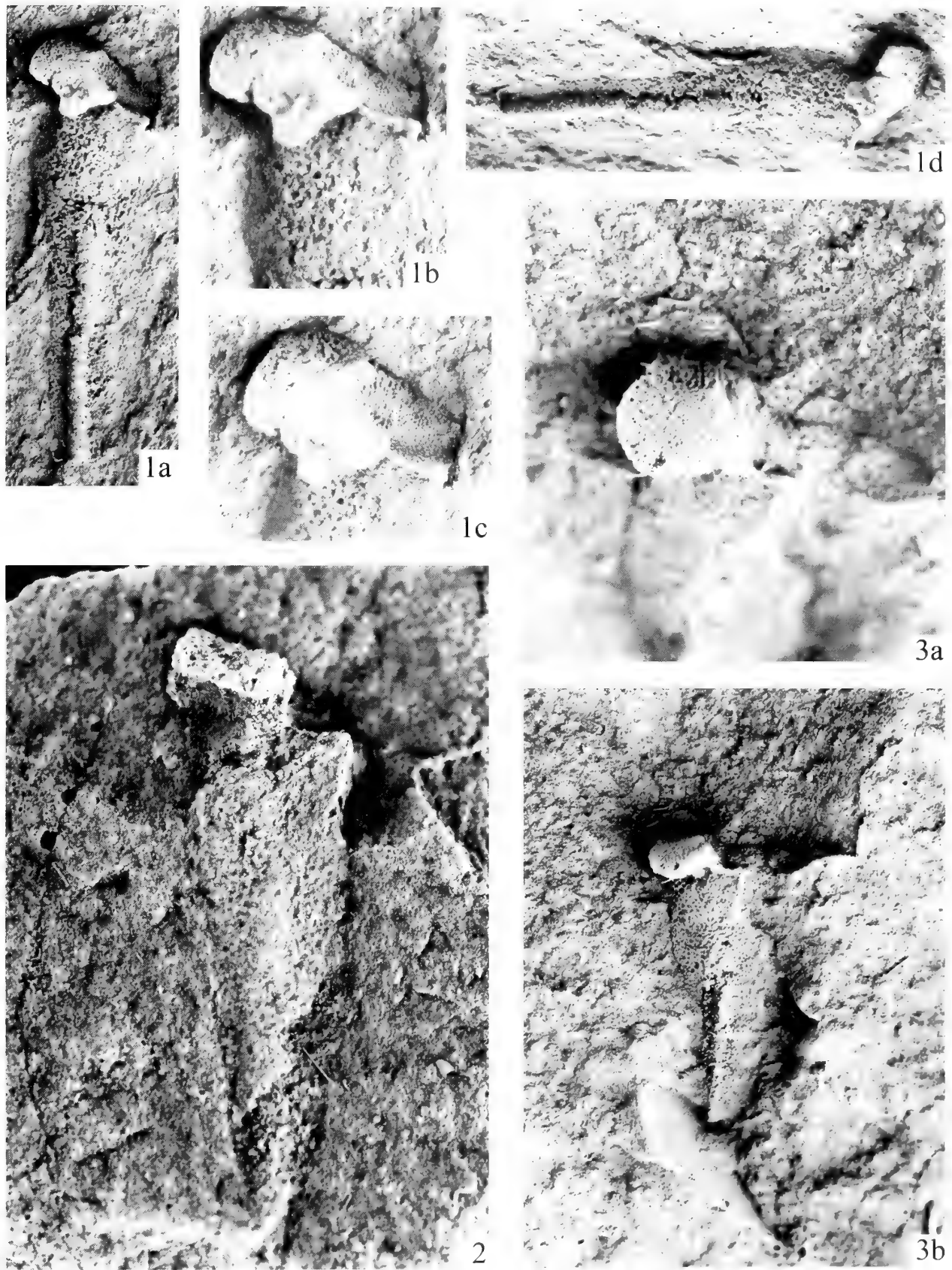
The dorso-lateral projection of M'_1 (Pl. 6, figs 1–3) has a broadly trapezoidal outline and is gently convex both longitudinally and, to a lesser extent, transversely. Its ventral half is almost vertical and bends sharply rearward to continue into the ventral surface of the plate. The dorso-lateral projection of M'_1 bends abruptly rearward at the level of the medial half of its dorsal margin giving rise to a stout,

dorsal wedge-like structure, slightly thicker medially than laterally and bearing a flat, tongue-shaped posterior process. The dorsal surface of this process slopes slightly downward both in a rearward direction and in a medio-lateral direction. The antero-medial part of the wedge-like structure is truncated, triangular in outline and flat-surfaced, and articulated with the left adoral plate (see above). The ventral apex of this articular surface contacts the lateral end of the crest-like, dorso-medial margin of the left apophysis. The postero-medial surface of the tongue-shaped posterior process is beak-like in outline and deeply excavated, whereas its postero-lateral surface is comparatively less expanded dorso-ventrally, less arcuate in plan view and convex outward. Its medial half slopes upward laterally and continues into the almost horizontal lateral half. Both surfaces merge ventrally into the trough-like thecal surface of the plate, which continues posteriorly into the dorsal surface of the zygial process.

The dorsal surface of the zygial process (Fig. 6; Pl. 6, figs 1–3) is flat or very gently convex in transverse section in its anterior quarter. The posterior three-quarters of it is occupied by a straight ridge which is slightly closer to the right margin of the zygial process than it is to its left margin. The ridge is wider and less pronounced in its

PLATE 6

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3143; **a**, **d**, $\times 12$; **b**, **c**, $\times 20$; dorsal aspect of plate M'_1 ; note dorso-lateral projection and apophysis of plate, and internal ridge on its dorsal surface. **2**, EE 3101, $\times 20$; internal ridge on dorsal surface of M'_1 . **3**, EE 3117; **a**, $\times 20$; **b**, $\times 10$; dorsal aspect of M'_1 .



anterior half than in its posterior half. Anteriorly, it appears to be very slightly raised above the level of the internal surface of the zygial process. Posteriorly, it becomes almost semicylindrical in shape. The transition between the anterior half and the posterior half is nearly abrupt. The anterior end of the ridge merges gradually into the internal surface of the zygial process.

STEREOM. Unlike the marginalia, all integument plates are made of a 2-dimensional stereom meshwork, consisting of regularly arranged, subcircular to subhexagonal pores separated by short trabeculae. The stereom fabric of the marginalia differs slightly from that of the dorsal and ventral integuments. In addition, the texture of the peripheral margin is more irregular than that of the remaining surface area of the marginalia.

There are indications that the suranal plate likewise consisted of a 2-dimensional meshwork, at least peripherally. However, the central part of this plate may have been formed by a 3-dimensional meshwork, albeit considerably less thick than the marginalia (e.g. Pl. 2, fig. 4). The stereom of the suranal plate is most characteristic in that it changes remarkably from the centre towards the periphery of the plate. The stereom texture of a roughly bell-shaped area of the external surface of the suranal plate comprised between its centre and its anterior margin is of the reticulate type observed in the supracentralia and infracentralia, although the size of the holes is on average slightly larger than in the integument plates. The size of the holes becomes progressively smaller towards the lateral margins and the antero-lateral angles of the plate, where the trabeculae are thicker and shorter than in its central part. The smallest size of the holes is observed at the level of a broadly crescentic area lying immediately anterior to the posterior margin of the plate, where the trabeculae seem to be flat-topped. Trabeculae and holes become more irregular, antero-posteriorly elongate and arranged according to a broadly fringe-like pattern along the posterior margin of the suranal plate. The fringe extends slightly posterior to the rearmost ends of the left and right parts of the thecal frame and consists of narrow, finger-shaped trabeculae of approximately equal length separated by elongate holes of variable length and outline. Rarely are adjacent trabeculae connected by thin, transverse rods or walls. The rearmost ends of the trabeculae are extremely variable in shape (spatulate, pointed or rounded), so that the fringe appears to have an irregular outline. The lateral ends of the fringe consist of remarkably short trabeculae with rare intercalated holes, and pass abruptly into the postero-lateral angles of the suranal plate.

The texture of the internal and external surface of both the supracentralia (Pl. 1, figs 2–5; Pl. 2, figs 2–4, 5; Pl. 3, figs 2, 4; Pl. 5, figs 1–2; Pl. 7, fig. 2, 4–5; Pl. 8, fig. 3) and the infracentralia (Pl. 2, figs 1, 3; Pl. 3, figs 1, 3, 5; Pl. 4, figs 1–2, 4) does not change remarkably, although in the case of the supracentralia, their internal surfaces show smaller, more irregular and more widely spaced pores than their external surface.

Changes in the stereom texture of the marginalia are best described by reference to the illustrations (e.g. Pl. 1, figs 2–5; Pl. 2, figs 4–5; Pl. 3, fig. 3; Pl. 6, figs 1–3; Pl. 7, fig. 2; Pl. 8, figs 1–2). I only point out that the most remarkable feature of the stereom of the inside

of the marginalia is the transverse elongation of some pores in the deepest portions of the trough-like internal excavations of the plates (e.g. Pl. 4, fig. 3).

Aulacophore

PROXIMAL PART. The proximal part of the aulacophore is invariably disrupted or missing in the material studied (Pl. 1, fig. 2; Pl. 2, fig. 5; Pl. 3, figs 1, 3, 5; Pl. 5, figs 1–3; Pl. 7, figs 2, 6; Pl. 8, figs 1–2). Tectals and inferolaterals are likely to have formed two dorsal and two ventral longitudinal rows respectively, although their precise arrangement cannot be reconstructed accurately. In few specimens (e.g. Pl. 7, fig. 2), it is possible to observe three to four small segments aligned longitudinally despite the extensive disruption and partly overlapping each other, although the latter condition may represent an artifact of preservation rather than a genuine feature.

Some of the plates of the proximal aulacophore are strongly arcuate in transverse section and approximately square in outline. One of their two longest margins is gently convex whereas the other margin is slightly concave. The two shortest margins of the plates in question differ in length and shape; the shorter of these margins is straight, whereas the longer one is broadly concave and projects into a small conical process at one of its extremities.

By comparison with the proximal part of the aulacophore of *Reticulocarpus hanusi*, as reconstructed by Jefferies & Prokop (1972), I suggest that the arcuate plates in question may belong to the longitudinal ventral series and, therefore, may correspond to inferolaterals. If this interpretation is correct, the conical processes would occupy the ventral, antero-lateral angles of the arcuate plates, following the anatomical orientation adopted in this paper.

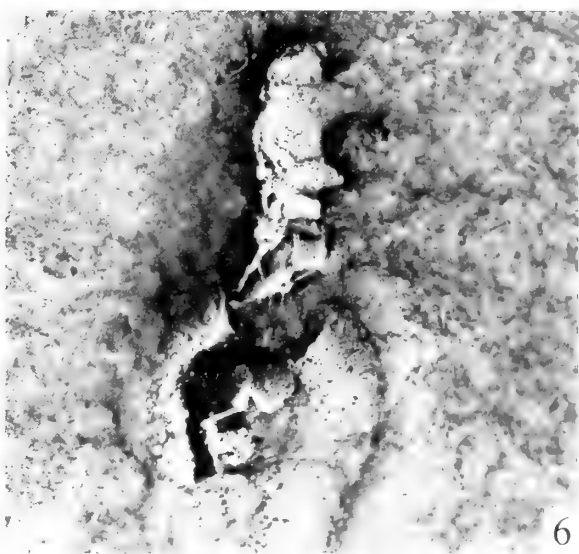
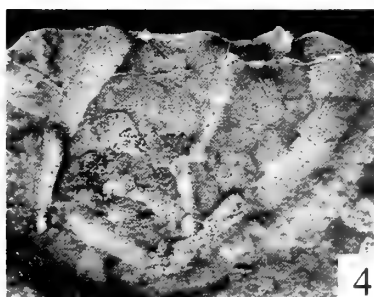
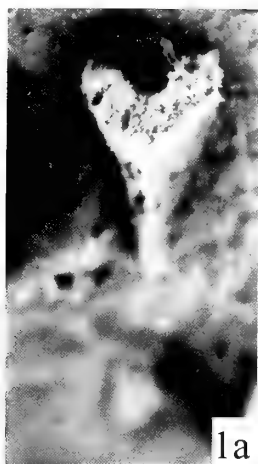
Another kind of plate is represented by slightly arcuate elements without conical projections and rectangular in outline (e.g. Pl. 1, fig. 2). These may belong to the longitudinal dorsal series and may thus correspond to tectals. As in *Reticulocarpus*, the plates of the proximal part of the aulacophore probably decreased in size to a small extent anteriorly. This is suggested by the fact that the posterior part of the styloid of *Juliaecarpus*, around which the most anterior tectals and inferolaterals were probably wrapped up in life, is just smaller than the thecal excavation for the aulacophore insertion.

It is impossible to say whether these two kinds of plates were sutured along their lateral and medial margins to form complete tetramerous rings or whether elements of the dorsal and/or the ventral longitudinal series were separate. Likewise, it is impossible to ascertain whether the plates formed opposite or alternate rows dorsally and/or ventrally. The presence of small intercalary plates, reported by Jefferies & Prokop (1972) in the proximal part of the aulacophore of *Reticulocarpus*, is difficult to document in *Juliaecarpus*. Small, subrhomboidal elements found in some specimens in the region of the proximal aulacophore may represent intercalary plates or fragments of tectals and inferolaterals (e.g. Pl. 5, figs 1–2).

INTERMEDIATE PART. The styloid is a robust structure, slightly longer than wide, consisting of a saddle-shaped posterior part and a

PLATE 7

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1a, b**, EE 3175, $\times 20$; posterior aspect of isolated ossicle; note changes in stereom structure along the spike. **2**, EE 3070, $\times 15$; complete but slightly flattened theca in dorsal aspect with poorly preserved aulacophore; note dorso-lateral projections of M'_1 and M_1 . **3**, EE 3141, $\times 10$; incomplete and heavily disrupted theca in dorsal aspect; note massive aspect of posterior zygial process in the centre of the photograph. **4**, EE 3184, $\times 5$; incomplete and slightly disrupted theca in dorsal aspect; note well-preserved and articulated supracentralia, and disrupted zygial bar. **5**, EE 3152, $\times 6$; poorly preserved theca in ventral aspect with damaged and displaced infracentralia. **6**, EE 3146, $\times 10$; poorly preserved aulacophore in right lateral view, with complete styloid and broken first ossicle articulated with it.



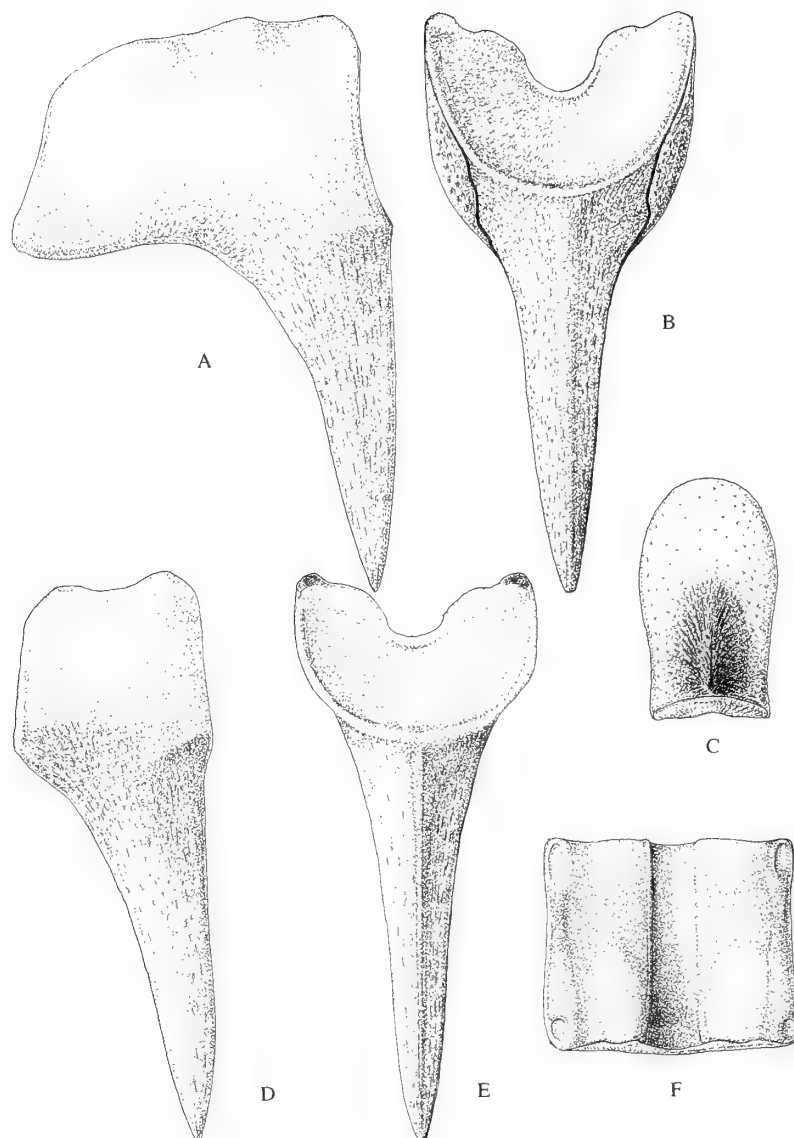


Fig. 7 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of external and internal aspects of styloid and of a proximal ossicle. **A**, right lateral view of styloid. **B**, anterior view of styloid. **C**, ventral view of styloid (much reduced with respect to A and B). **D**, right lateral view of ossicle. **E**, posterior view of ossicle. **F**, dorsal view of ossicle.

well developed anterior spike (Fig. 7A–C; Pl. 2, fig. 3; Pl. 3, figs 1, 3–4; Pl. 5, figs 1, 3–4; Pl. 7, fig. 6; Pl. 8, figs 1–2). The posterior part is gently arcuate ventrally in lateral view and is about as long as wide. Its ventral surface is approximately semicircular in cross-section. Its lateral surfaces are subparallel and slightly convex to flat in their uppermost part and decrease rapidly in height posteriorly converg-

ing into a broadly semicircular posterior margin. The latter forms the postero-ventral boundary of a circular excavation which occupies the posterior half of the styloid. The excavation lies on an oblique plane oriented at an acute angle with the horizontal plane.

The height of the spike is slightly greater than the total length of the styloid. The spike is gently curved backward near its apex,

PLATE 8

Juliaecarpus milnerorum gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. All latex casts coated with ammonium chloride. **1**, EE 3101, $\times 20$: close-up of aulacophore; note partly damaged styloid spike. **2**, EE 3070, $\times 20$: posterior half of ventral aspect of theca and poorly preserved styloid and ossicles. **3**, EE 3178, $\times 8$: almost complete, slightly compressed theca of an individual in dorsal aspect (bottom end of photograph), poorly preserved theca of a second individual in dorsal aspect (centre) and isolated plate M'_3 .



slightly compressed laterally, with blunt anterior and posterior margins, elliptical in cross-section throughout most of its height and roughly circular near its apex. Its lateral surfaces are gently concave in the upper two-thirds and merge smoothly into the posterior part of the styloid. Its posterior margin meets the posterior part of the styloid along a smooth, hyperbolic curve in lateral view.

DISTAL PART. Isolated ossicles and paired plates are observed in some specimens (Fig. 7D–F; Pl. 2, fig. 3; Pl. 3, figs 1, 3, 5; Pl. 5, figs 3–4, 6; Pl. 7, figs 1, 6; Pl. 8, figs 1–2). In a few individuals, the distal part of the aulacophore is preserved articulated and straight and consists of two or three segments. However, it is not absolutely certain that a short distal aulacophore represents a genuine feature of *Juliaecarpus*. Jefferies & Prokop (1972) argued in favour of the presence of a reduced distal aulacophore (their hind tail) in *Reticulocarpus hanusi* (see also below). Although it is possible that the aulacophores of both *Reticulocarpus* and *Juliaecarpus* consisted of a greatly reduced number of segments in comparison with those of other stylophorans, it is risky to deduce their original length from the available material.

As noted by Lefebvre *et al.* (1998), the distal part of the stylophoran aulacophore is extremely fragile and often incompletely preserved. In addition, because the distal aulacophores of both *Reticulocarpus* and *Juliaecarpus* seem to have been rigid, it is likely that they broke up rather easily during diagenesis or burial and that its various segments were dragged away from the rest of the body. It is possible, therefore, that more distal ossicles were present in life.

As in the case of the styloid, each ossicle consists of an upper, massive part and a lower, recurved spike. The massive part is just wider than long and composed of anterior and posterior articular surfaces, two lateral surfaces and an upper surface. The anterior and posterior articular surfaces are subequal in shape and size and roughly crescentic. The posterior surface is flat except for the presence of a poorly developed ridge occupying the central third of its lower margin. The anterior surface is slightly depressed in its lower half and shows no ridges. The lower margins of both the anterior and the posterior surfaces are accurately semicircular. Their upper margins are complicated by the intersection of both articular surfaces with the system of longitudinal grooves and thickenings present on the upper surface of the massive part. The lateral surfaces of the massive part are very gently convex in transverse section and broadly rectangular in outline, and diverge slightly lateralward in dorsal direction. They merge gradually into the lateral surfaces of the spike from which they are separated by a very low, almost indistinct subhorizontal ridge disappearing rapidly anteriorly. The upper surface of the massive part is deeply concave and carries a median longitudinal furrow (Ubaghs, 1968) with a broadly parabolic cross-section. The furrow is flanked by a left and a right thickening, about half as wide as the groove and with a blunt, gently convex top. The thickenings are asymmetrical in cross-section, for they slope slightly upward in a medio-lateral direction. The most lateral parts of the upper surface are generally poorly preserved. However, it is possible to see the presence of left and right bump-like projections about half as long as the ossicles and slightly displaced anteriorly. Immediately posterior to these projections are very shallow, straight transverse channels, slightly diverging posteriorly from the median longitudinal furrow and apparently intersecting the lateral thickenings.

The ossicular spike is almost twice as high as the massive part and laterally compressed for most of its height, so that its cross-section appears to be subelliptical. Near its apex, the spike is more rounded in section and ends in a subconical point. The anterior and posterior margins of the spike are narrowly acute in section, although never acutely sharp, and concave in lateral profile, the posterior margin

more so than the anterior margin. In lateral view, the uppermost part of the posterior margin forms a small angle with the posterior articular surface of the massive part. As a result, the spike points almost exactly ventralward rather than posteriorly as in *Reticulocarpus*. In their upper third, the lateral surfaces of the spike are gently concave, whereas at the level of their lower third they are mostly flat and subparallel. The distance between the anterior and the posterior margin of the spike decreases rapidly dorso-ventrally.

The paired plates of the distal aulacophore are not preserved in place. However, I interpret as disarticulated plates several small, subcircular to plectrum-shaped elements with a characteristic radial striation pattern. These are visible in proximity to the ossicles in some specimens (e.g. Pl. 8, fig. 1). The margin of the plates towards which the striae radiate out may correspond to their anterior side, although this is not certain.

STEREOM. The plates of the proximal part of the aulacophore display a retiform stereom similar to that of the centralia and marginalia, although the average size of the perforations is much smaller. The perforations are apparently distributed regularly on the surface of the plates. Those plates which are here interpreted as inferolaterals show a radiating pattern of trabeculae separated by elongate pores in their posterior half.

The stereom texture of the ossicles (Pl. 5, fig. 3; Pl. 7, fig. 1; Pl. 8, fig. 1) differs in the massive part and along the height of the spike. As far as the massive part is concerned, its anterior, posterior and upper surfaces, as well as the upper parts of its lateral surfaces, show a compact stereom, with no apparent texture pattern. The stereom texture is reticulate at the level of the upper half of the lateral surfaces of the spike, whereas its anterior and posterior margins and the apex show an irregularly perforated to coarsely granular texture consisting of short trabeculae and shallow pits. The stereom of the paired plates is mostly reticulate, but becomes compact or granular along their margins.

FUNCTIONAL MORPHOLOGY

General considerations

INTRODUCTION. Despite several claims to the contrary (e.g. Jefferies, 1984, 1986 and references therein), a consensus on the functional morphology of the stylophorans (or on any other aspect of their palaeobiology) has not yet been reached (Ruta, 1998, in press). Although some inferences are plausible (e.g. Jefferies & Prokop, 1972; Daley, 1992; Woods & Jefferies, 1992; Donovan, in press), they do not necessarily imply the correctness of the life-style interpretations proposed for these animals. Ubaghs (1968) provided the most comprehensive summary of the various functional hypotheses put forward so far (see also Ubaghs, 1981; Jefferies, 1986 and Kolata *et al.*, 1991).

In this section, the functional adaptations of the theca (including its dorsal and ventral integuments) and suranal plate of *Juliaecarpus* are analyzed and the significance of certain anatomical features (especially the lateral profile of the theca) in relation to the stability of the animal in water currents is examined in detail.

A brief account of the possible functions of the aulacophore (feeding organ; locomotory device) is dealt with in the next two sections and a reconstruction of the locomotory cycle of *Juliaecarpus* is presented.

FUNCTIONAL ADAPTATIONS OF THE THECA. Before discussing the external anatomy of *Juliaecarpus* from a functional viewpoint, it is necessary to consider briefly the ankyroid *Reticulocarpus hanusi*,

the biomechanics and locomotion of which were analyzed in great detail by Jefferies & Prokop (1972). It is reasonable to apply some of Jefferies & Prokop's (1972) arguments also to *Juliaecarpus*, given the fundamental anatomical resemblance between the latter and *Reticulocarpus* (see also the section on morphological comparisons below).

According to Jefferies & Prokop (1972), *Reticulocarpus* was fundamentally adapted to staying up on a soft sea-bottom, aided in this by the weight-bearing capacity of the muddy substrate rather than by compensation through lateral displacement of the sediment (see also Jefferies, 1975, 1981 for a discussions of the biomechanical constraints imposed by the two methods in different stylophorans). The following morphological features of *Reticulocarpus* suggest such a life-style: 1) flat ventral surface of the theca; 2) nearly bilaterally symmetrical outline; 3) perforated texture of the stereom; 4) presence of a peripheral flange; 5) small size. Jefferies & Prokop (1972) considered these features to be adaptations for reduction of the total skeletal mass of the animal, reduction of its weight per unit area and even distribution of the body weight to the sediment through the flat ventral side of the theca.

The fact that the thecal outline of *Juliaecarpus* is more bilaterally symmetrical than that of *Reticulocarpus* implies that in *Juliaecarpus*, the thecal weight may have been distributed to the sediment more uniformly than in *Reticulocarpus* and in approximately equal amounts on the left and on the right sides of the theca with respect to the oro-anal axis. A more bilaterally symmetrical outline may also have involved greater stability in the water currents and a more effective manoeuvrability of the theca during locomotion, when the animal pulled itself along dragged by its aulacophore (see below for a reconstruction of the locomotion in *Juliaecarpus*).

The lateral profile of the theca of *Juliaecarpus*, as reconstructed in this paper, appears to be very low and decreases progressively in height from the aulacophore insertion to the anal opening (see anatomical description above). In addition, neither the supracentralia nor the marginalia show projections or irregularities of any sort. With a certain approximation, such a low, almost smooth lateral profile is similar to the cross-section of a hydrofoil.

This observation suggests that, perhaps, water turbulence was drastically reduced or even absent all around the theca of *Juliaecarpus*. A regularly laminar, or almost laminar, water flow may have contributed to stabilize the animal in a regime of currents, perhaps supplementing the anchoring action of its styloid and ossicular spikes (see below). Slowing down of the flow at the level of the theca/aulacophore junction (where the theca reached maximum thickness) or even production of eddies immediately above this region may have resulted in a slight increase in the fluid pressure (Bernoulli effect), thus preventing forces generated by the water currents from lifting the theca off the sea-floor. A similar hydrodynamic mechanism counteracting the action of currents, based on a series of flume tank experiments, was proposed by Daley (1996) for the North American Middle Cambrian solute *Coleicarpus sprinklei*.

The smaller size of the lateral denticulations of M'_2 and M_2 of *Juliaecarpus* with respect to those of *Reticulocarpus* and the less developed peripheral flange may have represented further adaptations to weight reduction, although this conclusion is not certain.

Stability in water currents, especially when *Juliaecarpus* was at rest on the sea bottom, was perhaps achieved in part through the suction forces acting along the flat, ventral surface of the theca. Suction forces, although not hampering the movements of the animal along the sea bottom, probably prevented its theca from tilting (see below). It is possible that, as in the case of other cornutes (e.g. see Daley, 1992), the zygial bar of *Juliaecarpus* may have helped reduce suction forces during the lateral power strokes of the aulacophore

(see reconstruction of the locomotory cycle below), presumably by interrupting the continuity of the smooth, ventral integument.

Thus, it is proposed that suction forces may have played an important role in stabilizing the animal in water currents, acting along the flat, ventral projections of the marginalia. At the same time, however, such forces had to be reduced in part when the animal pulled itself along the sea-floor. Reduction may have occurred essentially along a direction following the course of the zygial bar and was most important at its anterior end, near the theca/aulacophore insertion, where forces exerted by the lateral pushing movements of the aulacophore were transmitted to the theca.

INTEGUMENTS. It is not clear to what extent the dorsal and ventral integuments of *Juliaecarpus* were flexible in life. The occurrence of broad, almost polygonal plates that did not overlap each other (especially on the dorsal integument) certainly accounts for reduced flexibility. The integument is remarkably different from that of certain primitive cornutes (e.g. several boot-shaped forms), in some of which it consisted largely or exclusively of small, round or subpolygonal elements, presumably partly embedded in a soft tissue and not abutting against each other. Some degree of flexibility may have developed along the peripheral margins of the dorsal and ventral integuments of *Juliaecarpus* and in the portion of the dorsal integument lying immediately anterior to the suranal plate.

However, compression or expansion of the integuments was perhaps limited by the constructional morphology of the supracentralia and infracentralia. In fact, flexibility may have been limited to restricted portions of the integuments (e.g. the periproctal region or the integumental periphery) in most if not all ankyroids. In these, the integument plates usually grew larger than in the asymmetrical cornutes and, in some cases (e.g. Cripps, 1989a; Ubaghs, 1991; Cripps & Daley, 1994), the integuments consisted of few, large polygonal elements.

THE SURANAL PLATE AS A VALVE. The modalities of articulation of the suranal plate of *Juliaecarpus* with the posterior part of the thecal frame and with the supracentralia, and the fact that the lateral margins of this plate seem to have been blunt in cross-section, suggest that the suranal plate was probably capable of a certain degree of vertical movement in life, perhaps acting as a flexible lid to seal partially the anal opening and control waste disposal, or as an aid in the regulation of gas exchanges through a pumping action of the gut (Prof. R. L. Parsley, pers. comm.).

That the suranal plate may have played an important role in gas exchange is plausible, considering the fact that the theca of *Juliaecarpus* does not show openings other than the posterior anus. Primitive cornutes display a diverse array of body openings (e.g. sutural pores, cothurnopores, lamellipores, etc.; see Ubaghs, 1968) which are likely to have functioned as respiratory structures (see elaboration of this argument in the chordate interpretation of stylophorans provided by Jefferies, 1986).

Unlike primitive cornutes, ankyroids rarely display thecal openings (apart from the anus). Thus, the evolutionary history of stylophorans may have witnessed a shift in the gas exchange functions from the thecal pores to other parts of the body (e.g. anus, integument, appendage). The perforated stereom of the integuments and, perhaps to a lesser extent, that of the marginalia and of the aulacophore may also have been involved in gas exchange, although this argument is highly speculative.

The aulacophore as a locomotory device

As stated in the introduction, I regard the aulacophore as the homologue of an echinoderm ambulacrum (Sumrall, 1997). However, I

also believe that most, if not all of the stylophorans used their aulacophores as a locomotory organ.

I agree with Jefferies & Prokop (1972) that the hollow nature and perforated stereom texture of the ossicles, paired plates and styloid in such stylophorans as *Reticulocarpus* may have represented further adaptations for reducing body weight. However, as already explained above, I question the validity of their arguments concerning the occurrence of a short aulacophore. As discussed in the anatomical description, none of the observed specimens of *Juliaecarpus* shows the inside of the styloid and of the ossicular spikes. Therefore, their hollow nature, although plausible, cannot be corroborated by direct observations. In addition, their stereom texture is less porous than that of *Reticulocarpus*.

I concur with Jefferies & Prokop (1972), Jefferies (1975, 1981, 1984, 1986), Jefferies *et al.*, 1987, Woods & Jefferies (1992) and Cripps & Daley (1994) that several morphological features of the stylophorans indicate that they may have moved in the direction of the appendage (i.e. anteriorly according to the anatomical orientation adopted in the present work). As pointed out by Cripps & Daley (1994), the articulated appendage may also have had an anchoring function. As in the case of *Reticulocarpus* and *Prokopicystis* (and most other cornute stylophorans), the distal part of the aulacophore of *Juliaecarpus* must have behaved as a rigid, rod-like structure in life, as suggested by the presence of flat interossicular articular surfaces.

The aulacophore of *Juliaecarpus* could probably move horizontally and vertically thanks to the high degree of flexibility of its proximal region. As in other stylophorans, the bulk of the musculature was probably concentrated in the lumen of the articulated rings of the proximal part of the aulacophore, which probably represented the main motor during locomotion (Jefferies & Prokop, 1972; Jefferies, 1984, 1986; Jefferies *et al.*, 1987; Woods & Jefferies, 1992).

Contrary to Jefferies & Prokop (1972) and Jefferies (1986), however, I consider vertical thrusts of the styloid and ossicular spikes within the sediment to have been poorly effective for movement (as indicated by the fact that the spikes are mostly flattened laterally and show a slightly pronounced keel posteriorly), but highly effective to cut a way open through the mud. Lateral movements of the partially buried intermediate and distal parts of the aulacophore, on the other hand, may have resulted in a more effective lateral pushing action against the substrate. This is because during the lateral thrusts, the entire lateral surfaces of the styloid and ossicular processes were in contact with the mud. The power strokes were made more effective by the rigid articulations between adjacent ossicles and between the most proximal ossicle and the styloid. This functional interpretation is applied also to *Reticulocarpus*.

To sum up, left and right lateral thrusts can be visualised as power strokes exerting an alternating clockwise and anticlockwise 'rowing' action, whereas return strokes consisted mainly of vertical, upward and downward movements enabling the animal to free its aulacophore from mud and to lower it down within sediment. Ruta & Bartels (1998) have recently suggested that a similar alternating series of vertical thrusts (presumably not actively involved in locomotion) and lateral thrusts (exerting a dragging action) occurred in the locomotory cycle of the anomalocystitid mitrate *Rhenocystis latipedunculata* Dehm, 1932 from the Lower Devonian of Germany.

I hypothesize that, at the beginning of each lateral push within the sediment, the theca of *Juliaecarpus* rotated slightly in a direction opposite to that of the thrust and slightly forward (anatomically anterior). As explained below, this yawing component of the movement was probably reduced by the elongation of the theca and by the fact that its centre of mass was likely to be close to the thecal

aulacophore insertion. The position of the theca was perhaps readjusted at the beginning of the successive power stroke, when the 'rowing' action of the aulacophore exerted a lateral thrust in the opposite direction with respect to that of the preceding power stroke.

It is possible that the comparatively more elongate theca of *Juliaecarpus* and its higher degree of bilateral symmetry with respect to *Reticulocarpus* prevented excessive yaw while the animal pulled itself along on the surface of the sea floor (for a comparison with the functional adaptations in mitrates see the comprehensive discussion of the biomechanics of these animals in Jefferies, 1984). That yaw was reduced during locomotion is also suggested by the fact that the centre of mass of the theca of *Juliaecarpus* probably lay somewhere at the level of its anterior half, where the thecal frame reaches its maximum height and width and the where the marginalia are comparatively thicker than in more posterior parts of the theca. This region, being close to the theca/aulacophore insertion, was perhaps less likely to swing laterally about a hypothetical vertical axis passing through the anterior thecal excavation.

Rolling and pitching components of the movement were presumably greatly reduced or even absent. This is mainly due to the fact that if, as I believe, locomotion was achieved essentially through lateral thrusting actions of the intermediate and distal parts of the aulacophore (*contra* Jefferies & Prokop, 1972 and Jefferies, 1986 but in partial agreement with the conclusions presented by Jefferies *et al.*, 1987, Daley, 1992 and Woods & Jefferies, 1992), then no vertical components of the reaction forces of the sediment to the movements of the aulacophore could be transmitted to the theca.

It is possible that such vertical components were slightly more effective when the aulacophore was lowered down within the mud or extracted from it. However, in the downward thrust, the pointed processes of the styloid and ossicles presumably penetrated through the superficial layers of mud with minimum effort. Furthermore, the aulacophore moved essentially through the uppermost layers of the sediment in the upward thrust, where cohesion forces acting between particles of mud were strongly reduced by the high water content.

Thus, friction was negligible during the vertical movements of the aulacophore, because of the slashing action of the spikes and because of the relatively high fluidity of the sediment. The reaction forces to the vertical thrusts exerted by the latter, therefore, were presumably weak. In addition, the flat ventral side of the theca and the occurrence of lateral flanges in *Juliaecarpus* probably prevented or greatly reduced the tilting of the theca (see also above), thus reducing the risk of it sinking into the substrate (for analogous adaptations in other cornutes see Jefferies & Prokop, 1972, Jefferies *et al.*, 1987, Daley, 1992, Woods & Jefferies, 1992 and Cripps & Daley, 1994).

In conditions of maximum ventral flexion of the proximal part of the aulacophore, the spike-like processes pointed backward, or backward and slightly downward. Thus, *Juliaecarpus* may have anchored itself more firmly, for the whole appendage was inserted within relatively dense layers of sediment well below the level of the sea bottom. Such a posture may have been effective in a regime of occasional and particularly strong water currents. Friedrich (1993) proposed a similar anchoring function for the appendage of cinctan echinoderms.

In conclusion, the locomotory cycle of *Juliaecarpus* can be visualized as a series of clockwise and anti-clockwise lateral thrusts of the stiff, intermediate and distal parts of the aulacophore within mud, alternating with vertical movements in the water column, perhaps a few microns off the surface of the sea-floor (Fig. 8). A wide variety of movements could be performed through combination of horizontal and vertical flexions of the tetrameric rings. A clockwise lateral thrust was probably followed by an upward lift of the appendage (which was thus released from the mud), by its partial rotation in an

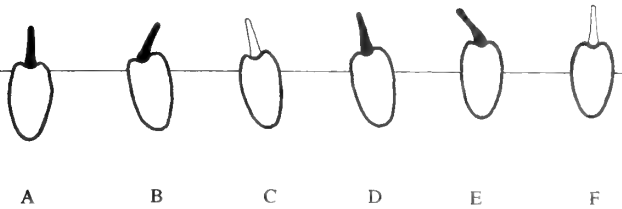


Fig. 8 *Juliaecarpus milnerorum* gen. et sp. nov. Late Ordovician, Upper Ashgill, Rawtheyan, Upper Ktaoua Formation, Morocco. Reconstruction of a hypothetical locomotory cycle. The horizontal black line is an imaginary reference direction. **A**, locomotion begins: the aulacophore is lowered down within mud and represented by a blackened rod. **B**, first power stroke: the aulacophore is pushed rightward against mud while the theca yaws slightly anti-clockwise and moves forward while pivoting on its left antero-lateral angle. **C**, first return stroke: the aulacophore (represented by a white rod) is freed from mud and rotated leftward. **D**, the aulacophore is lowered down within mud. **E**, second power stroke: the aulacophore is pushed leftward against mud while the theca yaws slightly clockwise and moves forward while pivoting on its right antero-lateral angle. **F**, second return stroke: the aulacophore is freed from mud and rotated rightward.

anti-clockwise direction (perhaps bringing the aulacophore parallel to the oro-anal axis), by a downward thrust within the sediment (facilitated by the shape of the styloid and ossicles), and finally by a lateral pushing action within the mud in an anti-clockwise direction. During alternating clockwise and anti-clockwise lateral thrusts, the theca of *Juliaecarpus* probably yawed very slightly about a vertical axis passing through or close to the theca/aulacophore insertion, so that its antero-lateral angles moved slightly anterior.

However, yawing, rolling and pitching components of the movements were perhaps negligible, so that the theca was relatively stable during locomotion. The lateral flanges of *Juliaecarpus* may have partially prevented sliding of the theca in a posterior direction, although their poor development in comparison with those of *Reticulocarpos* indicates that they were probably scarcely effective as friction-generating devices.

I point out that, as in previous reconstructions of the locomotory cycle of stylophorans (see especially Jefferies, 1984 and Woods & Jefferies, 1992), no accurate estimate of the speed and of the distance covered by the animal at the end of each power stroke can be provided. Therefore, the position occupied by *Juliaecarpus* at the end of a cycle is only speculative.

Based on the relative proportions of the theca and of the preserved part of the aulacophore I conclude that, as in the case of other cornutes (and perhaps of all stylophorans), locomotion in *Juliaecarpus* was probably not very advantageous from an energy point of view, although it may have allowed the animal to explore adjacent, food-rich patches of the sea-floor (see the next section) and to have changed its position with respect to the water currents. In summary, the life-style of *Juliaecarpus* was perhaps that of a relatively sedentary, suspension and/or detritus feeding, bottom dwelling organism (see also Parsley, 1988, 1991, 1994, 1997, 1998).

The aulacophore as a feeding organ

With regards to the feeding function of the aulacophore, I accept Parsley's (1988, 1991) view that this structure was probably oriented upstream in the main direction of the water current when the animal fed. *Juliaecarpus* may have exploited food sources in the proximity of its body by moving the rigid, distal part of the appendage laterally, a few microns off the substrate.

With its aulacophore held straight in the water current, *Juliaecarpus* perhaps fed by allowing food particles to enter through the slit-like spaces present between adjacent pairs of distal aulacophore plates. Mitrates, on the other hand, seem to have been able to exploit food particles in suspension more actively than cornutes.

The aulacophore of mitrates (including its distal part) was characterized by a higher flexibility than that of cornutes. According to Parsley (1988, 1991; but see comments in Kolata *et al.*, 1991 and Ruta, 1998, in press), mitrates could arch the distal aulacophore so as to increase the spaces between consecutive segments (the paired cover plates of their distal aulacophores were apparently fused along their medial margins, thus strengthening the whole appendage and making it more effective as a locomotory organ when it pushed against mud).

As explained in the anatomical section, whether the cover plates of the distal aulacophore of *Juliaecarpus* could open in life (as in the case of the cornute genus *Phyllocystis* Thoral, 1935 and few other stylophorans) is difficult to ascertain (Ubahgs, 1968, 1969, 1981; Jefferies, 1968, 1986). It is also proposed that the stirring action exerted by the styloid and ossicular spikes may have brought particulate food in suspension.

The recurved styloid and ossicular spikes of *Juliaecarpus* probably enhanced the gripping action of the aulacophore by pointing in the direction opposite to that of the water current flow (i.e. the spikes would point in a downstream direction) when the animal fed by holding its appendage in the currents.

Waste disposal was perhaps facilitated by slight vertical movements of the suranal plate (see above) and by the fact that, given the position of the animal in the water currents, its faeces were dragged away from the body at the rear end of the theca.

COMPARISONS

Similarities and differences in the thecal plating and aulacophore

In this section, *Juliaecarpus* is compared in detail with a number of other ankyroid stylophorans. Such comparisons do not aim to identify shared derived features, although they provide a taxonomic framework for a revised phylogeny of these organisms. As specified in the introduction, a formal numerical character analysis of the stylophorans is not presented in this work.

Among the cornute-like stylophorans placed by Parsley (1997, 1998) in his order Ankyroida, the genera *Reticulocarpos*, *Beryllia* and *Domfrontia* are discussed at length here, for they show closer resemblance to *Juliaecarpus* than other ankyroids do. I also briefly compare *Juliaecarpus* with *Nanocarpus*, which represents a generalized ankyroid with several skeletal features foreshadowing the morphological condition found in later, presumably more derived stylophorans.

Juliaecarpus is similar to *Reticulocarpos hanusi* from the Llanvirn of Bohemia (Fig. 9) in the general aspect and proportions of the theca, in the shape and relative lengths of the marginalia and in the morphology of the styloid and ossicles. However, external anatomical differences between these two taxa are numerous and can be summarized as follows:

1. The thecal outline of *Juliaecarpus* is more bilaterally symmetrical than that of *Reticulocarpos*. Corresponding pairs of marginalia, especially the more posterior ones, are almost equal in shape and length and the oro-anal axis is almost aligned with the longitudinal axis of the aulacophore. In addition, the lateral thecal margins

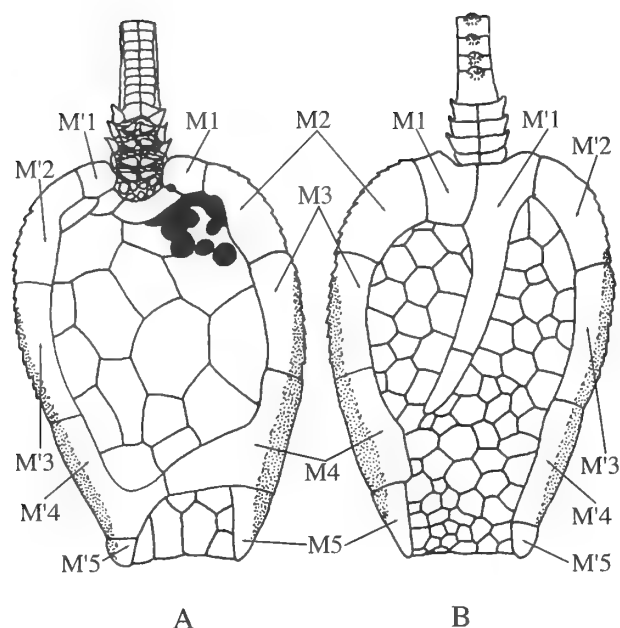


Fig. 9 *Reticulocarpus hanusi* Jefferies & Prokop. Middle Ordovician, Llanvirn, Sárka Formation, Czech Republic. Schematic reconstruction of external aspect. A, dorsal view. B, ventral view (redrawn and modified after Jefferies & Prokop, 1972 and Cripps & Daley, 1994).

of *Juliaecarpus* show their maximum degree of curvature at the level of plates M'_2 and M_2 , whereas in *Reticulocarpus*, such margins are more strongly convex at the level of M'_3 and M_3 , on the right side of the theca, and of M'_2 and M'_3 , on its left side. In addition, the dorso-lateral projections of the marginalia of *Juliaecarpus* are slightly to much wider than their ventral projections, whereas in *Reticulocarpus*, the difference in width between the two kinds of projections is much smaller.

2. Unlike *Reticulocarpus*, *Juliaecarpus* possesses a large suranal plate. This plate is probably not unique to *Juliaecarpus*, as I shall explain below, because an enlarged plate occupying the posterior part of the dorsal integument seems to have been present also in *Beryllia* and *Domfrontia* (see discussion of these genera below).
3. In *Juliaecarpus*, plates M'_4 and M_4 do not send medial projections forming a dorsal bar as in *Reticulocarpus*. In the stylophoran phylogeny presented by Parsley (1997, 1998), the presence of a dorsal bar characterizes a clade uniting *Reticulocarpus*, *Prokopicystis* and *Hanusia*, contrary to the hypotheses of relationships presented by Cripps (1991) and Cripps & Daley (1994) (but see also Daley, 1992).
4. Plates M'_2 and M_2 of *Juliaecarpus* are less strongly convex laterally than their namesakes in *Reticulocarpus* and their dorso-lateral projections are slightly wider than those of more posterior marginalia. The dorso-lateral projections of M'_2 and M_2 contribute only in part to the antero-lateral angles of the theca, whereas in some other ankyroids (but not in *Reticulocarpus*), these marginalia send more strongly developed medial branches forming most of the antero-lateral angles of the theca.
5. The length of the posterior process of M'_1 in *Juliaecarpus* is almost twice the length of the posterior zygial plate; such a process is also slightly wider than the ventral projections of the marginalia throughout its length and its posterior end lies slightly

posterior to the suture between M_1 and M_4 and slightly anterior to that between M'_3 and M'_4 . In *Reticulocarpus*, on the other hand, the M'_1 process is comparatively shorter and stouter than that of *Juliaecarpus* and its posterior half is less wide than the ventral projections of the marginalia; furthermore, its posterior end lies anterior to both the M_3/M_4 and the M'_3/M'_4 sutures. In addition, the posterior zygial plate of *Reticulocarpus* probably did not contact the thecal frame (see discussion below).

6. The lateral margins of M_2 and M'_2 in *Juliaecarpus* carry shallow denticulations, as opposed to the pronounced, saw-like serrations present along the lateral margins of M_2 , M'_2 , M_3 and M'_3 in *Reticulocarpus*.
7. Plates M'_5 and M_5 of *Juliaecarpus*, assuming their correct identification, are comparatively much smaller than their namesakes in *Reticulocarpus* and much narrower than more anterior marginalia. In *Reticulocarpus*, these plates also differ in shape and size, whereas in *Juliaecarpus*, they are almost mirror images of each other.
8. In *Juliaecarpus*, the transition from the retiform stereom texture on the median part of the dorso-lateral projections of the marginalia to the striated texture on the peripheral flange is more gradual than in *Reticulocarpus* and no cancellose or irregular stereom is interposed between these two kinds of textures.
9. The peripheral flange of *Juliaecarpus* is less developed than that of *Reticulocarpus* and appears to have possessed comparatively shallower lateral fringes and less irregular trabeculae; in addition, it seems to have been confined mainly to the anterior half of the lateral margins of the thecal frame.
10. Some of the supracentralia of *Juliaecarpus*, especially those on the anterior half of the dorsal integument, approach a bilaterally symmetrical arrangement and it is always possible to distinguish some larger plates in a central position flanked by longitudinal rows of smaller plates comprised between the marginal frame and the oro-anal axis. Conversely, the supracentralia of *Reticulocarpus* are not arranged according to a particular pattern.
11. The spike-like processes on the styloid and ossicles of *Juliaecarpus* are comparatively less high, less recurved and more laterally flattened than those of *Reticulocarpus* and pointed almost exactly downward rather than downward and rearward in life. The stereom texture of the styloid and ossicles is slightly more compact and consists of comparatively smaller perforations in *Juliaecarpus* than in *Reticulocarpus*.

The internal aspect of the theca permits more limited comparisons between *Juliaecarpus* and *Reticulocarpus*. At the level of the zygial bar, the most obvious difference between these two genera is the fact that in *Juliaecarpus*, the ridge on the dorsal surface of the zygial process of M'_1 does not extend as far forward as in *Reticulocarpus*, in which such a ridge reaches the suture between M_1 and M'_1 . The preservation of the internal side of M_1 and M'_1 in *Juliaecarpus* is not as detailed as in *Reticulocarpus*. A comparison between the reconstruction of these plates in *Juliaecarpus* and the reconstruction provided by Jefferies & Prokop (1972) for *Reticulocarpus* highlights major differences in the morphology of this region of the theca in the two ankyroids.

Two other stylophorans, *Beryllia miranda* and *Domfrontia pissotensis*, both from the Llandeilo of France, reveal interesting similarities with *Juliaecarpus*. As in *Juliaecarpus*, some of the supracentralia of both *Beryllia* and *Domfrontia*, especially those aligned along the oro-anal axis, are slightly to much larger than the remaining supracentralia. In the case of *Beryllia*, the supracentralia which occupy the anterior third of the dorsal integument are

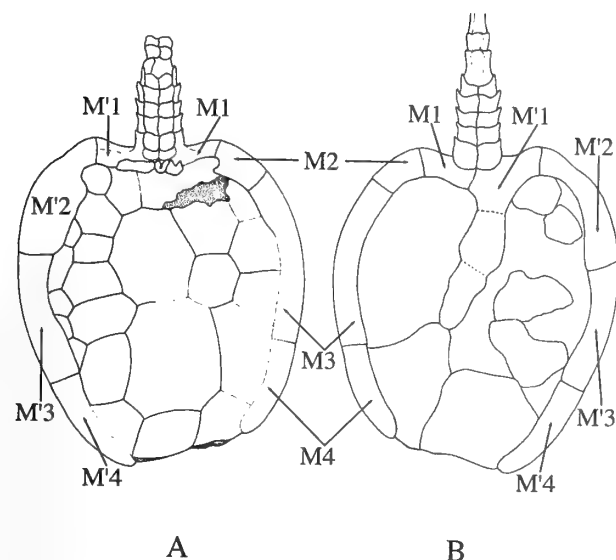


Fig. 10 *Beryllia miranda* Cripps & Daley. Middle Ordovician, Llandeilo, Pissot Formation, France. Schematic reconstruction of external aspect. **A**, dorsal view. **B**, ventral view (redrawn and modified after Cripps & Daley, 1994).

arranged in broadly transverse rows (e.g. Cripps & Daley, 1994: pl. 2, fig. 5).

In the reconstruction of *Beryllia* provided by Cripps & Daley (1994), the thecal frame shows four left and four right marginal plates (M'_5 and M_5 are presumably absent) (Fig. 10). In the same reconstruction, a subpentagonal and an irregularly parallelogram-like plate of subequal size appear along the posterior margin of the dorsal integument and roof over the obliquely oriented anal opening.

However, at least one of the specimens of *Beryllia* figured by Cripps & Daley (1994: pl. 2, fig. 5) shows a transversely expanded, subrectangular supracentral plate between the posterior ends of M'_4 and M_4 . The plate in question carries an irregular fringe along its posterior margin and the average size of its stereom mesh pores is slightly larger than that of other dorsal integument plates. It may be homologous with the suranal plate of *Juliaecarpus* but its outline and relative position with respect to the surrounding plates are poorly defined.

The following skeletal features distinguish *Juliaecarpus* from *Beryllia*:

1. Higher thecal length/width ratio. Based on the measurements provided by Cripps & Daley (1994), *Beryllia* shows a thecal length/width ratio of about 1:2, as opposed to the ratio value of 1:72 reported in *Juliaecarpus*.
2. Smaller length difference between the left and the right lateral thecal margins, accompanied by more bilaterally symmetrical thecal outline and less oblique position of the anal opening. In *Beryllia*, the theca is slightly asymmetrical, due to length difference between the left and the right marginalia. Such difference characterizes all cornute-like ankyroids and indicates that the process of symmetrization of the thecal outline must have preceded the acquisition of paired marginalia of equal (or subequal) shape and size. *Juliaecarpus* exemplifies a stage of this process, in that the presence of an almost bilaterally symmetrical theca is accompanied by almost complete symmetrization of the more posterior pairs of marginalia, whereas the anterior marginalia

(especially M'_2 and M_2) are still markedly different (see also comparison with *Nanocarpus* below).

3. Less pronounced convexity of lateral thecal margins (see also point 2 above).
4. Lesser elongation of M_3 with respect to other marginalia (see also point 1 above).
5. Dorso-lateral projections of marginalia wider than their ventral projections (see also point 1 in the comparison with *Reticulocarpus*).
6. Greater difference in shape and size between the ventral projections of M_1 and M_2 . The ventral projections of these marginalia appear to be subequal in *Beryllia*, but markedly different in *Juliaecarpus*.
7. Much smaller difference in length between M'_2 and M_2 (see also point 2 above).
8. Slenderer, straighter and comparatively more elongate zygial process of M'_1 (see also discussion of this structure below).
9. Less clear demarcation between M'_1 and its zygial process. While in *Beryllia* the posterior zygial process of M'_1 widens abruptly in its anterior part to become confluent with this plate, in *Juliaecarpus* the boundary between M'_1 and its process is less clearly evident (see description of the internal surface of this plate above).
10. Adoral plates longer than wide and separated by a leftward concave suture. The occurrence of a median adoral in *Beryllia* is possible, based on the poor material figured by Cripps & Daley (1994). The left and right adoralia of *Beryllia* are wider than long and, in comparison with those of *Juliaecarpus*, they are much smaller than the dorso-lateral projections of M'_1 and M_1 .
11. Apparently larger number of broad, polygonal, more regularly arranged plates on the anterior third of the ventral integument. In *Beryllia*, only a few large polygonal supracentralia in a subcentral position are visible. These are flanked by irregularly shaped plates, apparently more numerous on the left than on the right. As pointed out in the anatomical description above, the supracentralia of *Juliaecarpus* form transverse rows of elements arranged in a bilaterally symmetrical (or nearly so) pattern on the anterior half of the dorsal integument (see also point 11 in the comparison with *Reticulocarpus*).
12. Strongly developed, recurved, spike-like styloid and ossicular processes. The styloid and ossicles of *Beryllia* possess low, poorly pronounced keel-shaped longitudinal processes, clearly different from the conical processes of *Juliaecarpus* (see also point 11 in the comparison with *Reticulocarpus*).

The material of *Domfrontia* is less well preserved than that of *Beryllia*, but it does permit limited comparisons with *Juliaecarpus*. As in the case of *Juliaecarpus* and *Beryllia*, it is difficult to ascertain the precise number of lateral marginal plates, due to the poor preservation of the rearmost ends of the thecal frame (Fig. 11).

The inside of what I interpret as a possible suranal plate is partly visible in the holotype of *Domfrontia* (Cripps & Daley, 1994: pl. 1, fig. 5). The right part of such a plate, assuming its correct identification, is hidden by one of the rearmost preserved infracentralia. The visible portion of it shows a more regular outline than the suranal of *Juliaecarpus*, a less extensive posterior fringe attached to an apparently semielliptical posterior margin and an almost straight, thickened anterior margin. However, unlike the suranal of *Juliaecarpus* and, perhaps, *Beryllia*, the like-named plate of *Domfrontia* does not seem to show a remarkably different stereom texture with respect to other integument plates.

The most important morphological differences when *Domfrontia* is compared with *Beryllia* and *Juliaecarpus* are as follows:

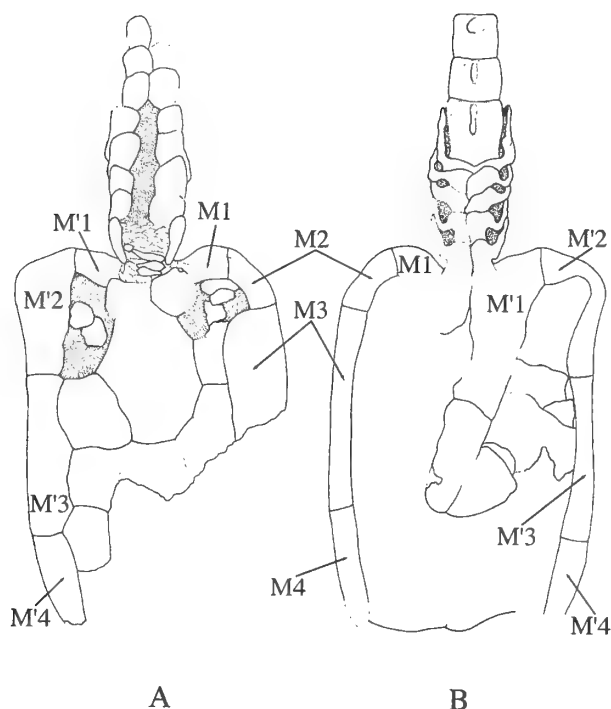


Fig. 11 *Domfrontia pissotensis* Cripps & Daley. Middle Ordovician, Llandeilo, Pissot Formation, France. Schematic reconstruction of external aspect. **A**, dorsal view. **B**, ventral view (redrawn and modified after Cripps & Daley, 1994).

1. According to the reconstruction provided by Cripps & Daley (1994), *Domfrontia* possesses almost straight lateral thecal margins. As a result, the anal opening is approximately as wide as the theca. Proportions and relative lengths of the marginalia of *Domfrontia* are similar to those of *Beryllia*, but differ remarkably from those of *Juliaecarpus*. The convexity of the lateral thecal margins of *Juliaecarpus* is somewhat intermediate between that of *Beryllia* and that of *Domfrontia*.
2. The zygial process of M'_1 in *Domfrontia* is comparatively wider and shorter than that of both *Beryllia* and *Juliaecarpus*. Likewise, the preserved part of the posterior zygial plate of *Domfrontia* suggests that this plate is stouter in this ankyroid than in the other two genera.
3. The styloid and ossicles of *Domfrontia* are shaped like bulges with a subelliptical to subcircular outline and carry a poorly defined median longitudinal keel with a semicircular to parabolic profile.
4. The ventral projection of M_1 is expanded posteriorly in *Domfrontia*, but not in *Beryllia* and only to a very limited extent in *Juliaecarpus*.

The number of marginal plates in such genera as *Juliaecarpus*, *Reticulocarpus*, *Beryllia* and *Domfrontia*, as well as their relative position and shape, gives support to Parsley's (1991, 1997, 1998) suggestion that several lineages within the ankyroids underwent reduction in the number of marginalia through decrease in size and subsequent loss of the rearmost plates. A brief comparison with the ankyroid *Nanocarpus dolambii* Ubaghs, 1991, from the lower Ordovician of southern France is interesting in this respect (Fig. 12).

Except for asymmetries in the thecal frame due to the relatively small size of M_2 and elongation of M'_3 , the theca of *Nanocarpus* is

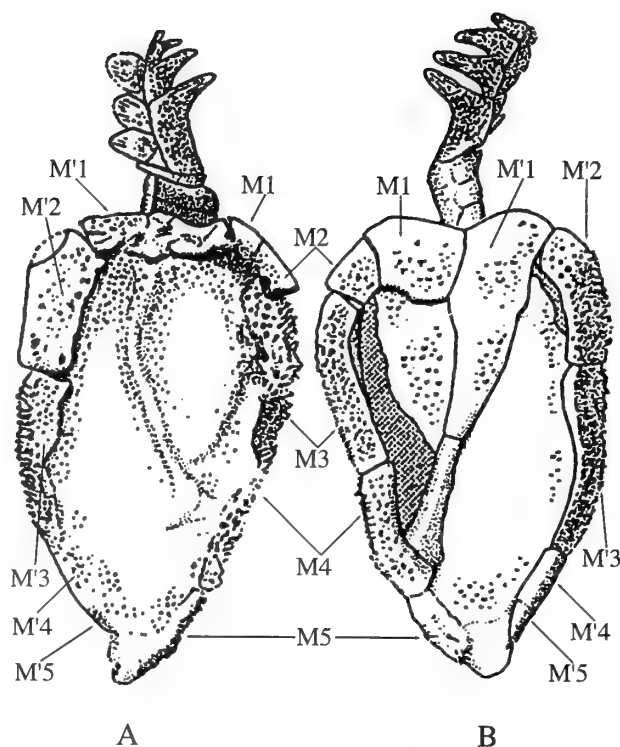


Fig. 12 *Nanocarpus dolambii* Ubaghs. Lower Ordovician, Lower Arenig, Schistes de Saint-Chinian, France. Schematic reconstruction of external aspect. **A**, dorsal view. **B**, ventral view (redrawn and modified after Ubaghs, 1991).

similar to that of *Juliaecarpus*. From a purely morphological point of view, *Nanocarpus* can be considered as a fairly generalized cornute-like ankyroid in which the theca retained asymmetries as in more primitive cornutes. In *Nanocarpus*, the rearmost marginalia, especially M_5 , are still relatively large with respect to more anterior marginalia, as opposed to the situation observed in *Reticulocarpus* and *Juliaecarpus*. On the other hand, M'_4 and M_4 are shorter than M'_3 and M_3 , and M'_2 and M_2 differ greatly in size.

An interesting feature observed in some of the specimens of *Nanocarpus* figured by Ubaghs (1991) is the presence of a posterior plate visible between M'_5 and M_5 . Although poorly preserved, this element seems to be homologous with the suranal plate of *Juliaecarpus*. However, it is difficult to say whether it was flexibly articulated with the rest of the thecal frame in life.

It is possible to hypothesize that, in the evolutionary history of the ankyroid stylophorans, thecal asymmetries were drastically reduced through the loss of the posterior marginalia, subsequent elongation of the marginalia occupying an intermediate position along the lateral margins of the thecal frame and, finally, acquisition of a more bilaterally symmetrical outline. A suranal plate, as explained below, may have been acquired in a number of ankyroids through enlargement and rearward displacement of a posterior supracentral plate which became flexibly articulated both with the dorsal integument and with the medial margins of the dorso-lateral projections of the most posterior marginalia.

As far as the ventral surface of the theca is concerned, the posterior zygial plate and posterior zygial process of *Nanocarpus* are similar in shape and general proportions to those of *Juliaecarpus*, except that in *Nanocarpus*, the posterior zygial process of M'_1 is slightly curved

and decreases rapidly in width distally and the posterior end of the posterior zygial plate is comparatively wider than in *Juliaecarpus*.

Suranal plate and stylophoran orientation

The occurrence of a well developed suranal plate in *Juliaecarpus* and, perhaps, also in *Beryllia* and *Domfrontia* (see discussion above) requires further comments on the orientation of cornutes (including cornute-like ankyroids) with respect to mitrates. Workers supporting the chordate interpretation of stylophorans (synthesis in Jefferies, 1986) homologize the plano-concave surface of the mitrate theca with the dorsal side of the cornute theca. Given this orientation, it may be argued that the suranal plate is homologous with the subanal plate observed in such early mitrates as *Chinianocarpus thoralis* Ubahgs, 1961, *Peltocystis cornuta* Thoral, 1935 and, perhaps, *Vizcainocarpus dentiger* Ruta, 1997 (see also Ubahgs, 1968, 1969). In these mitrates, the subanal plate occupies the posterior part of the plano-concave surface of the theca and floors the anal opening. As in the case of the suranal plate, there are indications that, at least in *Chinianocarpus* and *Peltocystis*, the subanal plate was flexibly articulated with the theca (Ubahgs, 1969).

In their discussion of the phylogenetic position of *Reticulocarpus* and the origin of mitrates, Jefferies & Prokop (1972) proposed that one of the supracentralia lying close to the mouth opening in derived, mitrate-like cornutes increased in size and gave rise to either the large subanal of such primitive mitrates as *Chinianocarpus* and *Peltocystis* (and, perhaps, *Vizcainocarpus*) or the rearmost element of the plano-concave surface of other mitrates (e.g. mitrocystitids and anomalocystitids; see also Ruta 1998, in press).

However, as already explained in the introduction, the bulk of anatomical evidence (arguments in Ubahgs, 1981, Kolata *et al.*, 1991, Parsley, 1991, 1997, Sumrall, 1997 and Lefebvre *et al.*, 1998), based mainly on a comparison between the aulacophore, adoral plates, apophyses and zygial/septum complex of cornutes and the like-named structures of mitrates, strongly supports the convex-side-up orientation of the mitrates as well as the homology between the convex surface of their thecae and the dorsal side of the cornute thecae.

Therefore, I regard the suranal plate of *Juliaecarpus* as a modified posterior dorsal integument plate, not homologous with the subanal plate of certain primitive mitrates. The suranal plate was perhaps not unique to *Juliaecarpus*. I tentatively suggest that its occurrence may represent a shared derived feature of a group of ankyroids including *Juliaecarpus*, *Beryllia* and *Domfrontia*. From the morphological comparisons outlined above, it is clear that these taxa show certain skeletal features in common. Enlargement of supracentralia on the posterior part of the dorsal integument (forming or not an almost regular spatial arrangement) and reduction or loss of the most posterior pair of marginalia are other possible shared characters of this group. A close relationship of these ankyroids with the clade (*Hanusia* + (*Reticulocarpus* + *Prokopicystis*)) (all these genera share a dorsal bar; see Parsley, 1997, 1998) is possible, considering the overall similar proportions and morphological characters of the theca and aulacophore in *Juliaecarpus* and *Reticulocarpus*.

However, I point out that, according to Parsley's (1997, 1998) phylogenetic analysis, *Beryllia* is the sister taxon to a clade comprising *Chinianocarpus* and the peltocystids (including *Peltocystis* as the most basal representative of this group of mitrates; see also Jefferies, 1973, 1986 and Jefferies & Lewis, 1978). In addition, Parsley (1997, 1998) did not include in his analysis *Domfrontia*, ranked among the poorly known or incomplete taxa. Clearly, the mixture of primitive and derived features found in *Juliaecarpus* requires a substantial reassessment of the polarity of a number of characters.

Morphological variation in the zygial bar

Among the ankyroid stylophorans, the genera *Beryllia*, *Domfrontia*, *Prokopicystis* and *Reticulocarpus* differ from other representatives of this group in the morphology of their zygial bar. The unusual configuration of this structure in the above-mentioned taxa deserves further considerations.

Reticulocarpus, *Prokopicystis* and *Domfrontia* were reconstructed as having an incomplete zygial bar (Jefferies & Prokop, 1972; Cripps, 1989a; Cripps & Daley, 1994). In particular, *Reticulocarpus* seems to have had a small somatic plate (posterior zygial plate) attached to the posterior zygial process of M'_1 . In Cripps' (1989a) reconstruction of *Prokopicystis*, only the posterior zygial process of M'_1 seems to have been present and no trace of a posterior plate attached to it has been recorded. In their reinterpretation of *Domfrontia*, Cripps & Daley (1994) reconstructed the zygial bar of this stylophoran as being similar to that of *Reticulocarpus*.

However, with the possible exception of *Reticulocarpus*, the incompleteness of the zygial bar in *Domfrontia* and *Prokopicystis* is based on the interpretation of very poor material. None of the figured specimens of these two ankyroid genera clearly shows the boundaries of the posterior zygial plate. In a note published a few years before the formal description of *Reticulocarpus* by Jefferies & Prokop (1972) (Jefferies, pers. comm.), Ubahgs (1969) clearly stated that the zygial bar in two of the specimens of *Reticulocarpus* examined by him was apparently incomplete.

It is difficult to ascertain whether the incompleteness (if any) of the zygial bar is evidence of its progressive reduction and final disappearance in derived cornutes and, therefore, of the fact that the zygial/septum complex is not homologous in all stylophorans.

The peculiar zygial bar of *Beryllia* as reconstructed by Cripps & Daley (1994) suggests that this structure had a separate somatic plate in contact with a posterior right infracentral element, and that its anterior two-thirds comprised, in turn, a posterior plate and a short, stout process of M'_1 . Cripps & Daley (1994: 108) state that the strut of *Beryllia* is '... most clearly visible on NHM E63499a', but the figured specimen in question does not provide unequivocal evidence of a tripartite zygial bar. I re-examined the specimen in question and the remaining material of *Beryllia* in the collections of the London Natural History Museum. The specimens were cast using black-stained latex.

My own observations do not match Cripps & Daley's (1994). In particular, the zygial bar in NHM E63499 is too poorly preserved for its boundaries and general shape to be reconstructed. In particular, I could find no evidence of tripartition and no clear delimitation of the posterior zygial plate from the thecal frame. The impression left by the zygial bar on the dorsal integument of another specimen (NHM E63496b; Cripps & Daley, 1994: pl. 2, fig. 5) suggests that, in fact, the zygial bar of *Beryllia* had a slender shape and a sinuous course and that its rearmost end lay closer to the posterior right part of the thecal frame than in the reconstruction provided by Cripps & Daley (1994). In these respects, the bar is similar to that of such ankyroids as *Amygdalotheca griffiei* Ubahgs, 1969 from the lower Ordovician of southern France.

That the zygial bar of *Beryllia* may have consisted of a posterior process of M'_1 and of a posterior zygial plate is plausible, although not certain. However, I favour the latter interpretation, based in particular on the visible course of the bar in specimen NHM E63496b.

In summary, the specialized features of the zygial bar reported in several ankyroid species ought to be confirmed by discovery of better preserved material. *Juliaecarpus* shows the primitive condition for the ankyroids in possessing a posterior somatic plate articulated with the inner margins of the thecal frame. If my conclu-

sions are correct, the character distribution in above-mentioned ankyroids will have to be reconsidered, especially when the origin of mitrates from their cornute ancestors is taken into account.

CONCLUSIONS

Together with *Beryllia*, *Domfrontia* and *Reticulocarpos*, the new stylophoran *Juliaecarpus milnerorum* gen. et sp. nov. from the late Ashgill (late Rawtheyan) Upper Ktaoua Formation of Morocco ranks among the most bilaterally symmetrical stylophoran echinoderms. Following recent phylogenetic work by Parsley (1997, 1998), *Juliaecarpus* is an ankyroid, that is, a stylophoran with a separate zygial plate not belonging to the thecal frame and with well-developed, spike-shaped styloid and ossicular processes.

The most outstanding skeletal feature of *Juliaecarpus* is the presence of a large suranal plate flexibly articulated with the rear-most part of the thecal frame and dorsal integument. Such a plate may have enabled *Juliaecarpus* to regulate the pumping action of the gut by acting as a vertically movable, lid-like structure and to control waste disposal. A suranal plate was probably present also in the ankyroid genera *Beryllia* and *Domfrontia*, as suggested by the occurrence of a large, apparently continuous dorsal area revealing stereom structure at the posterior end of the theca.

A comparison with several ankyroids strengthens the view that, during the evolutionary history of the stylophorans, asymmetries in the thecal outline and in the marginalia, inherited from primitive (and often boot-shape) cornutes, became progressively less accentuated and were eventually lost in many forms (Ubaghs, 1968; Jefferies, 1986; Cripps, 1989b; Parsley, 1991, 1994, 1997, 1998; Ruta, 1998, in press). The acquisition of a progressively more bilaterally symmetrical thecal outline presumably preceded a complete symmetrization of the paired marginalia. Several stages of this process are exemplified by a number of cornute-like ankyroids. For instance, *Juliaecarpus* displays a high degree of bilateral symmetry in the theca, but asymmetries can still be observed at the level of some of the marginalia, especially M_1 , M'_1 , M_2 and M'_2 .

Acquisition of bilateral symmetry probably occurred several times independently in the stylophorans, as recent phylogenetic analyses and re-assessment of stylophoran thecal plate homologies suggest (Parsley, 1997, 1998; Lefebvre *et al.*, 1998; Dr B. Lefebvre, pers. comm.; Ms M. Marti-Mus, pers. comm.).

As in the case of *Reticulocarpos*, *Juliaecarpus* was probably capable of resting on the surface of the muddy sea-floor aided in this by the weight-bearing capacity of the sediment (Jefferies & Prokop, 1972). Nearly bilaterally symmetrical shape, small size, flat ventral surface of the theca, peripheral flange (albeit reduced in size in comparison with that of *Reticulocarpos*) and highly perforated skeletal plates all seem to account for this life-style.

Movement perhaps involved a downward thrusting and a lateral pushing action of the aulacophore within the sediment followed by an upward return stroke enabling the animal to free its aulacophore from the mud. Alternating clockwise and anti-clockwise lateral thrusts represented the active component of the locomotory cycle, whereas upward and downward movements, as well as lateral movement in the water column just above the sea-floor, allowed *Juliaecarpus* to readjust the position of its aulacophore between two successive power strokes. Several skeletal features of the theca and aulacophore suggest that yawing, rolling and pitching components of the movement were absent or much reduced.

Stability in the water currents was probably achieved through a combination of factors: 1) suction forces acting along the flat ventral

side of the theca; 2) reduction of water turbulence due to the low, gently convex lateral profile of the theca and possible production of eddies immediately above the theca/aulacophore junction, both effects resulting in water pressure increase (Bernoulli effect); 3) anchoring function of the recurved styloid and ossicular spikes, perhaps enhanced by the ability of the animal to bend the proximal part of its aulacophore ventralward and rearward to a considerable degree.

Juliaecarpus probably fed by holding its aulacophore upstream in the water current (see also Parsley, 1988, 1991). Food particles were brought in suspension by the stirring action of the aulacophore and forced to pass through the narrow spaces between adjacent pairs of cover plates.

Juliaecarpus adds to the taxonomic similarities between middle to late Ordovician faunas from Morocco and coeval faunas from several European regions. It also adds to the diversity of early cornute-like ankyroids, combines features of several previously described taxa and prompts a reassessment of the polarity of many characters within the stylophoran echinoderms. It is hoped that a revised character analysis of the whole group can yield information on the phylogenetic significance of this ankyroid.

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Late Cretaceous-early Tertiary echinoids from northern Spain: implications for the Cretaceous-Tertiary extinction event

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Synopsis. The Maastrichtian and Palaeocene echinoid faunas are described from Santander, Province of Cantabria, the Basque region of Spain and France, and the region around Irurtzun, Province of Navarra. These deposits range from shallow shelf carbonates to upper continental slope clastics. A total of 58 species are described, 40 from the Maastrichtian, nine from the Danian and nine from the Thanetian. Echinoid extinction is estimated to be around 40% in shallow water settings, but may have been more intense in deeper settings. Extinction levels are comparable with the other well-studied western European faunas of the Danish basin and the Limburg region. A striking shift in the geographic ranges of taxa took place between the end of the Cretaceous and the Palaeocene. Taxa migrated both from the Danish basin southwards and from the Tethyan region northwards at this time.

The first fossil representative of the Recent deep-sea family Aeropsidae is described from the early Thanetian of Navarra. New taxa described here include the genus *Sphenaster* and the species *Tylocidaris trempinus*, *Camerogalerus cantabrius*, *Adelopneustes ernsti*, *Stegaster palaeocenicus*, *Ovulaster reticulatus* and *Sphenaster larumbensis*.

INTRODUCTION

The end of the Cretaceous saw the extinction of many marine invertebrates, but precisely what events brought about this extinction, and over how short a time interval these events took place remain the subject of heated debate. Most research so far has been

directed towards documenting the synchronicity and duration of extinctions, through microstratigraphical sampling in 'complete' boundary sections (e.g. Marshall & Ward, 1996, MacLeod, 1998). Much less emphasis has been given to the ecological and geographical pattern of extinction at this time, with the notable exception of Jablonski & Raup (1994) and Smith & Jeffery (in press). Understanding what, if any, environmental pattern there is to survivorship

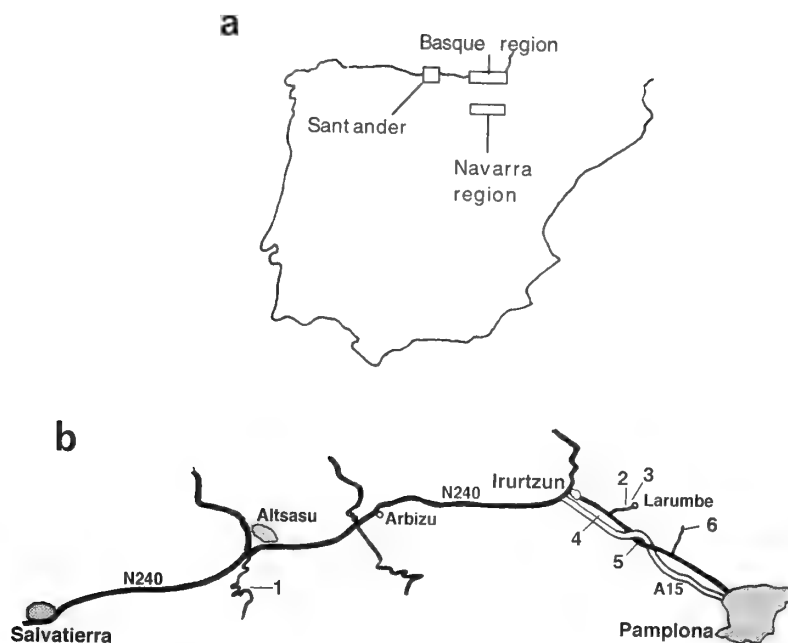


Fig. 1 Location maps. **a**, The three main areas in Spain and southern France from which the echinoid faunas are described. **b**, The location of the main echinoid-bearing horizons in the Irurtzun region, Navarra, studied in this paper. 1 = Olazagutia Pass; 2 = Casas de Oraien; 3 = Larumbe; 4 = Sarasate; 5 = Erice; 6 = Aristregui.

should help shed light on the immediate causes that led to the end Cretaceous extinctions.

We have been studying the echinoid faunas on either side of the Cretaceous – Tertiary boundary from three regions in Northern Spain. These faunas come from the open shelf sandy carbonate succession to the West of Santander, the continental slope deposits of the Basque region (Sopelana to Bidart), and the carbonate platform to intraplatform basinal facies around Irurtzun in the Province of Navarra (Fig. 1a). New collections from the Santander region (Gallemí, Jeffery & Smith), Basque region (Peter Ward) and Navarra region (Ernst, Gallemí, Jeffery & Smith) have been made, and the taxonomy updated and standardized. Using this new data we compare levels of extinction in the three faunas to see if there is any environmental signal. We also compare the level of extinction in northern Spain with that recorded from other European regions, specifically with Limburg and the Danish basin, to discover whether there is a latitudinal bias to extinction at this time. It has been shown that foraminifera suffered less intense extinction at higher palaeolatitudes (MacLeod & Keller, 1994, MacLeod, 1995) whereas no such pattern was evident for molluscs (Jablonski & Raup, 1994).

GEOLOGICAL SETTING

The late Cretaceous is represented by a wide range of facies and palaeoenvironments in the Basco-Cantabrian basin of northern Spain. By middle Campanian times this region formed a single flysch trough with lateral slope deposits, bordered by narrow shelf platforms. The southern margin of the evolving Biscay ocean developed as a series of pull-apart basins (Wiedman *et al.*, 1983) which became progressively more strongly affected by strike-slip tectonics to the east. Shallow-water carbonate facies developed across this narrow

shelf, with black shale facies forming in local basins. The Biscay trough extended approximately east-west along the line now formed by the Pyrenees. This oceanic arm, which is estimated to have had a palaeodepth of approximately 1,500 m (Delacotte, 1982), separated the shallow marine deposits of the Navarra-Cantabria platform to the south from the corresponding shallow shelf deposits of the South Aquitaine platform to the north-east.

There is a strong sea-level signature recognizable in the deposits of this region. Maastrichtian deposition falls within a single sea-level cycle (Wilmsen *et al.*, 1996). A major facies change occurs more or less coincident with the K-T boundary, brought about by rapid sea-level rise (Haq *et al.*, 1987, Keller *et al.*, 1993). During the Danian sea-level fell gradually, but began to rise once more in the late Thanetian. Climate towards the end of the Cretaceous was deteriorating (Barrera, 1994).

DETAILS OF SECTIONS

The Santander region

In the immediate vicinity of Santander, from Cabo Mayor westwards, Maastrichtian–Palaeocene sediments are exposed along the coastal cliffs (Fig. 2). The stratigraphy of this section has been studied in detail by Heredia *et al.* (1990) as part of the geological mapping of Cantabria. Here the Upper Campanian to Maastrichtian beds belong to the Cabo de Lata Formation (García-Mondéjar & Pujalte, 1982). The Maastrichtian part of the succession falls within a single sea-level cycle referred to as Megasequence 5 by Wilmsen *et al.* (1996). The basal beds comprise cross-bedded calcarenites with many hardgrounds and temporary hiatuses in sedimentation, and were deposited under falling sea-level. The presence of occasional tempestites suggests deposition within storm wave-base.

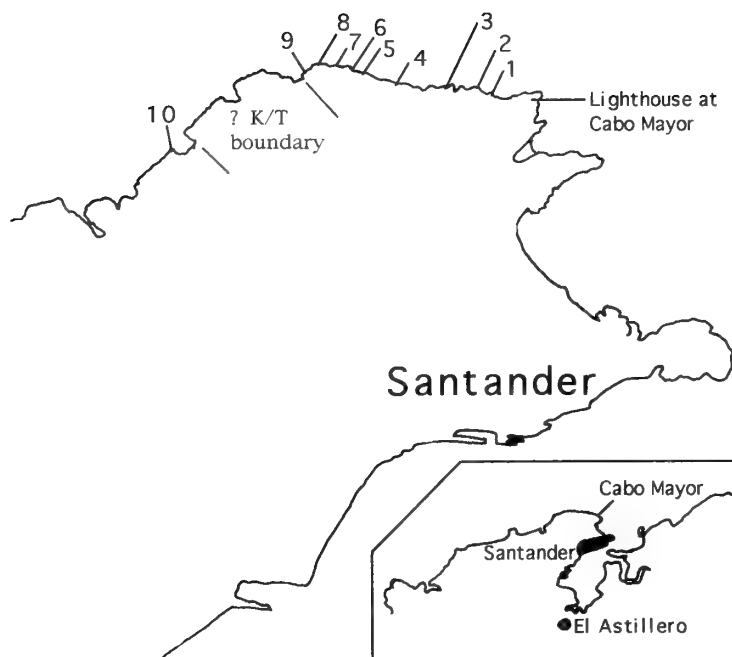


Fig. 2. Map showing the location of the main echinoid-bearing horizons in the Santander region, Cantabria, studied in this paper.

There then follows a thick succession of bedded sandy limestones, with thin calcarenitic limestones, and evidence of surge channels and tempestites (Wilmsen *et al.*, 1996), indicative of deposition within normal wave-base. This part of the succession was deposited under rising sea-level. There are a few thin conglomerates and shell-rich calcarenites which probably represent storm debris flows from near-shore habitats.

The upper beds become unfossiliferous, and return to a series of thinner bedded calcarenites and sandy limestones with abundant hiatuses and hardgrounds; they are dolomitized and were presumably emergent. Consequently, the boundary between the Maastrichtian and Palaeocene cannot be determined on faunal grounds. The dolomites and calcarenites together form the San Juan Formation, and have been attributed to the Danian and Montian. The succession is capped by a very thin series of calcarenites with glauconite, the Sancibrián Formation, which has a Thanetian microfauna (Heredia *et al.*, 1990).

In terms of depositional environment, the Cabo de Lata Formation represents relatively shallow inner platform clastics deposited within fair-weather wavebase (Heredia *et al.*, 1990). The presence of echinoids in these beds was first noted by Jiménez de Cisneros (1910) and Mengaud (1910), who correctly attributed these beds to the Maastrichtian. Jiménez de Cisneros (1912) listed the following echinoid species as coming from Santander: *Echinoconus conicus* Breynius [= *Galerites albogalerus* Klein], *Echinocorys vulgaris* Breynius, *E. conicus* Breynius, *Hemipneustes pyrenaicus* Hébert, *Hemiaster prunella* Desor and *Cidaridites* cf. *C. subvesiculosa* d'Orbigny. Later, Lambert (1920–22) identified five echinoids from

the Maastrichtian of this area; *Tylocidaris ramondi* Leymerie, *Conulus gigas* Cotteau, *Clypeolampas leskei* Goldfuss, *Hemipneustes pyrenaicus* Hébert and *Echinocorys terzensis* Lambert. Wilmsen *et al.* (1996) noted the presence of several echinoid events and listed a number of genera and species.

The San Juan Formation is interpreted as being deposited in a shallow, restricted internal platform setting, which becomes progressively less restricted upwards into the Sancibrián Formation.

Echinoids have been collected from 9 levels at ten localities along the cliff section west of Santander (Figs 2, 3).

The Basque region

Only deep-water Maastrichtian–Palaeocene facies are represented in the Basque region. During the early Maastrichtian continental slope turbidites were deposited. However, near the end of the early Maastrichtian there was a marked reduction in siliciclastic input, probably marking the world-wide late Maastrichtian regression. Following the K–T boundary there was an even more dramatic reduction in siliciclastic input to the basin, resulting in the deposition of pink coccolith limestones (commonly resedimented) during the Danian (Ward & Kennedy, 1993). Hiatuses and non-depositional surfaces are common in these Danian beds reflecting a major rise in sea-level.

From their study of coastal stratigraphical sections of the Zumaya–Algorri Formation at Sopelana, Zumaia, Hendaye and Bidart, Ward & Kennedy (1993) recognised five Maastrichtian units, referred to as Members I–V. Echinoids are found throughout the section 'but never in great abundance, and only rarely in bedding plane concentrations' (Ward & Kennedy, 1993). They are most common in Members IV and V. We have plotted the stratigraphic occurrence of echinoids from these localities onto a single standard section, Ward & Kennedy's (1993) Zumaia lithological section (Fig. 4).

The echinoid fauna from this region has not been studied since the

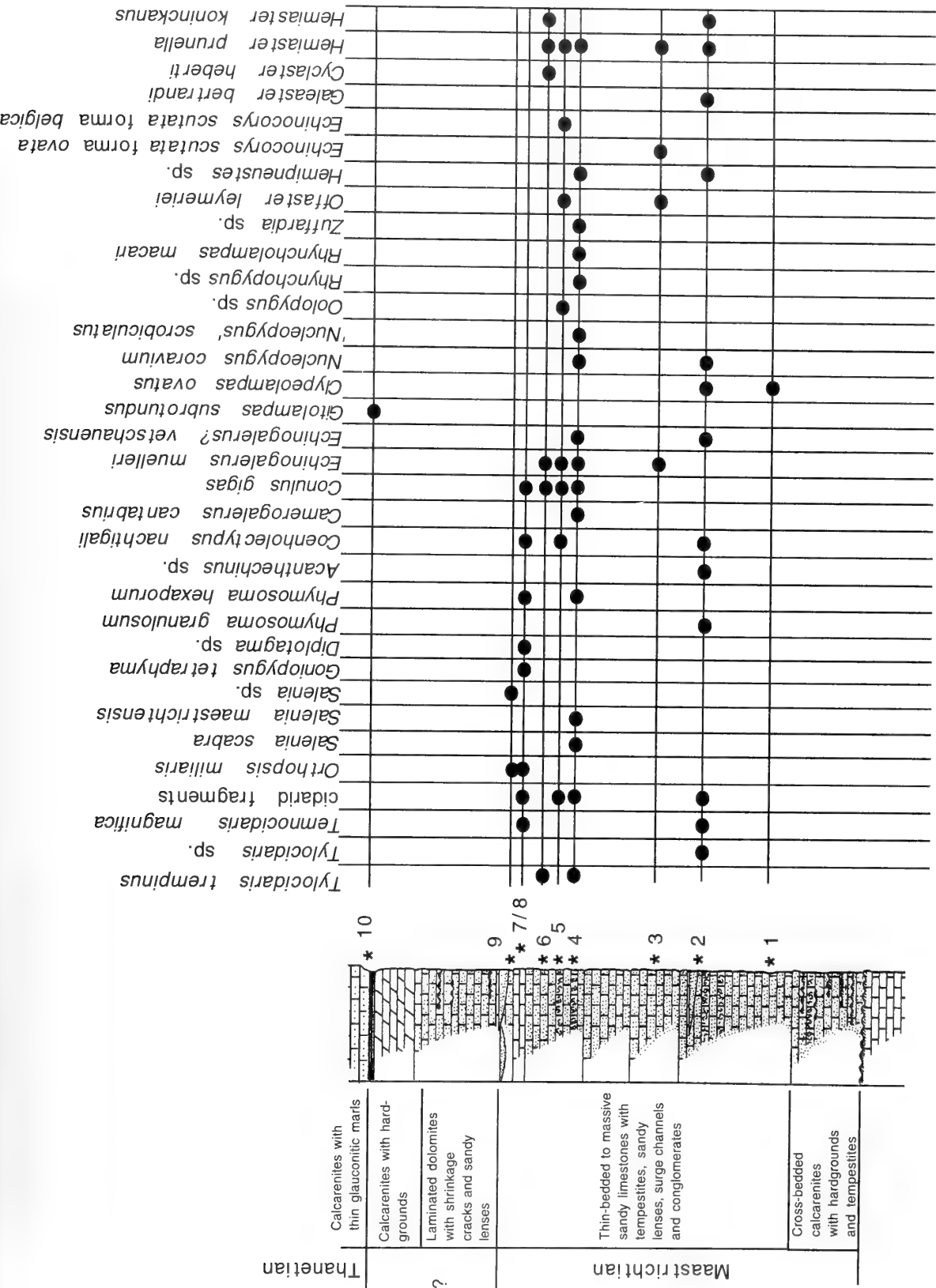


Fig. 3. Stratigraphic section of the Maastrichtian section to the West of Cabo Major, near Santander, Cantabria, showing the distribution of echinoids.

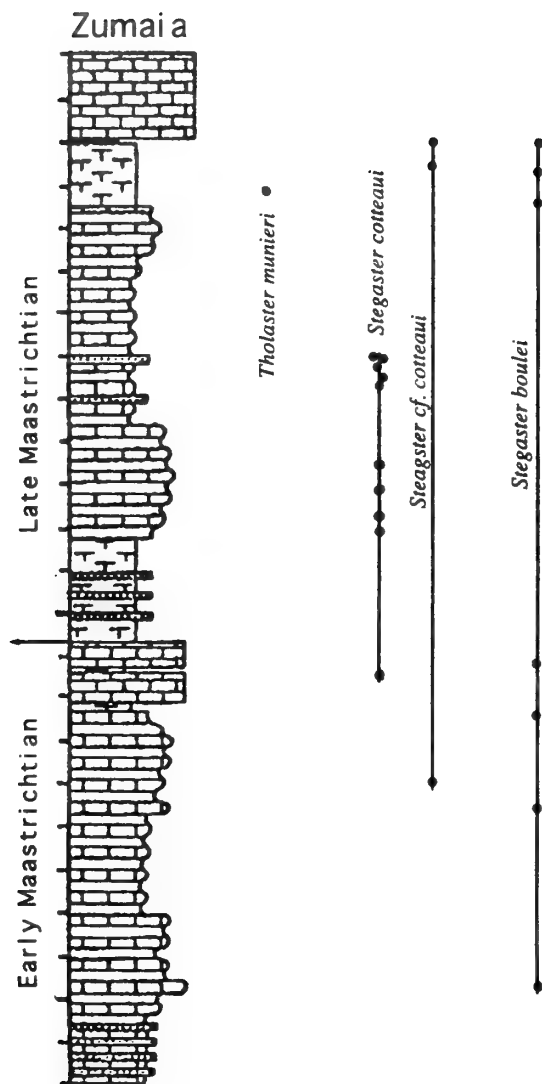


Fig. 4 Composite stratigraphic section of the Maastrichtian of the Basque region from Zumai a, Gipuzkoa, Spain to Bidart, Pyrénées-Atlantique, France (from Ward & Kennedy 1993) showing the distribution of echinoids.

pioneering work of Seunes (1888a, 1888b and 1889). He reported the occurrence of *Cidarid beaugeyi* Seunes, *Jeronia pyrenaica* Seunes, *Coraster beneharnicus* Seunes, *Echinocorys douvillei* Seunes, *Stegaster heberti* Seunes, *S. bouillei* Cotteau, *Gibbaster munieri* Seunes [= *Tholaster munieri* (Seunes)] and *Galeaster bertrandi* Seunes from the vicinity of Bidart.

The Navarra region

This has the most complicated geology of the three regions, being strongly affected by strike-slip faulting. Maastrichtian deposits are represented by two facies: shelf platform carbonates (studied at Olazagutia Pass) and shelf basinal mudrocks (studied at Larumbe and Sarasate) (Fig. 1b). Table 1 lists the echinoids collected from this region. The overlying Danian and early Thanetian consist of a sequence of coccolith limestones that in places includes reworked pebble beds.

Table 1 Echinoids from the Navarra district (see Fig. 1b for map of area).

LOCALITY 1. Maastrichtian, carbonate platform facies; Olazagutia Pass.

Tylocidaris (Sardocidaris) ramondi (Leymerie)
cidaroid plates indet.
Salenia (Pleurosalenia) maastrichtensis Schlüter
Conulus gigas (Cotteau)
Echinogalerus muelleri (Schlüter)
Nucleopygus scrobiculatus (Goldfuss)
Offaster leymeriei Cotteau
Hemipneustes pyrenaicus Hébert
Hemipneustes striatoradiatus (Leske)
Hemiaster koninckanus d'Orbigny
Hemiaster prunella (Lamarck)
Cyclaster sp.

LOCALITY 2. Late Thanetian, Casas de Oraien.

Gauthieria pseudomagnifica (Cotteau)
Adelopneustes ernsti sp. nov.
Cardiaster sp.
Isaster aquitanicus (de Grateloup)
Echinocorys scutata forma *cotteui* Lambert
Micraster tericensis Cotteau
Hemiaster stella (Morton)
Linthia sp. Cotteau

LOCALITY 3. Danian-early Thanetian at Larumbe.

Coraster vilanovae Cotteau
Coraster beneharnicus Seunes
Sphenaster larumba sp. nov.
Jeronia pyrenaica Seunes
Echinocorys sp.

LOCALITY 4. Maastrichtian; basinal facies.

Motorway cutting at Sarasate, just South-East of Irurzun.
Stegaster bouillei (Cotteau)
Stegaster altus Seunes
Echinocorys scutata forma *ovata* Leske
Ovulaster reticulatus sp. nov.
Pseudoffaster caucasicus (Dru)
Cyclaster sp.
Danian near summit of hill at Sarasate
Cyclaster aturicus (Seunes)
Cyclaster grindrei (Seunes)
Coraster beneharnicus Seunes

LOCALITY 5. Danian of Erice.

Coraster vilanovae Cotteau
Coraster beneharnicus Seunes
Cidaroid spines
Echinocorys scuata forma *pyrenaica* Seunes
Cyclaster grindrei (Seunes)

LOCALITY 6. Late Danian at Aristregui.

Stegaster paleocenicus sp. nov.
Jeronia pyrenaica Seunes
Coraster vilanovae Cotteau
Echinocorys scutata Leske

Olazagutia Pass. The carbonate platform succession was studied at Olazagutia Pass (Fig. 1b), the type locality of the Puerto de Olazagutia Formation (Amiot, 1982), along the road leading from Olazti to the Urbasa Range. The units that lie at the top of the Olazagutia Formation yield the richest and most varied fauna. These beds were deposited in an external platform setting (Amiot, 1982).

Here the Maastrichtian succession commences with a massive bedded limestone (Fig. 5). This is succeeded by a series of thinner sandy limestones, calcareous sandstones and marls which are richly fossiliferous. A thick sandy marl with a rich bryozoan fauna at the

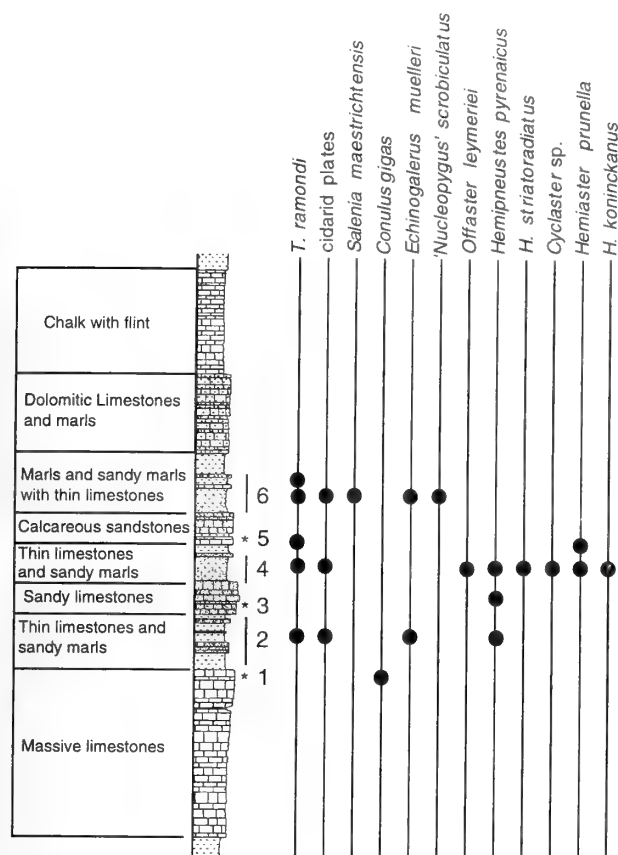


Fig. 5 Stratigraphic section through the Maastrichtian at Olazagutia Pass, Navarra, showing the distribution of echinoids.

top is followed by dolomitized limestones and more massive dolomites. The entire succession apparently represents a shallowing upward cycle, presumably correlatable with the upper part of the Cabo de Lata Formation in Santander.

This locality was first studied by Ruiz de Gaona (1943) who recorded a single echinoid (*Salenia*) from it. A detailed stratigraphic section was published by Amiot (*in Ciry et al.*, 1967) and its microfauna studied by Ramírez del Pozo (1971). Ramírez del Pozo recorded the following from this section: *Orbitoides media*, *Siderolites calcitrapoides*, *Lepidorbitoides socialis*, *Globotruncana contusa*, *Marssonella* cf. *trochus*, *Nummofallotia cretacea*, *Omphalocyclus macroporus* and *Racemigumbelina fruticosa*, amongst others, suggestive of a Late Maastrichtian age. A small number of echinoids have previously been reported from this section by Radig (1973).

Erice. A former limestone quarry on the northern side of the motorway A15 in the vicinity of Erice, exposes Cretaceous and Danian sediments. The succession commences with a series of alternating marly limestones and marls containing ammonites and large *Echinocorys*, considered to be Late Campanian in age. There is then a sharp break, probably representing a faulted contact, after which come a succession of deep-water, light-coloured limestones, in part conglomeratic, and locally showing slump fabrics. These are thick to medium-bedded at the base, but more thinly bedded upwards. The lower beds yield a fauna that includes *Coraster vilanovae*,

Cyclaster gindrei and *Echinocorys scutata* forma *pyrenaica*, that in this area characterizes the upper part of the Danian.

Sarasate. Alternating grey to blue (sometimes slumped) marly limestones and dark shales crop out immediately to the north of motorway A15 at the foot of Sarasate hill, south-west of the town of Irurtzun. Their macrofauna is limited to inoceramids, echinoids, less common brachiopods and rare ammonites, all of them attributed to the Maastrichtian. They were deposited in a shelf basin or shelf margin setting. Echinoids from here include *Stegaster altus* Seunes, *S. bouillei* Cotteau and *Echinocorys scutata* forma *ovata* Leske.

Higher up the hill (Astieso) there is a small outcrop of Danian limestone by the side of a forestry track which yields *Coraster* and *Cyclaster aturicus* Seunes.

Larumbe. On the eastern side of the village of Larumbe Maastrichtian black shales crop out. These have yielded fragments of *Stegaster* and an unidentified large spatangoid. As at Sarasate, these beds are interpreted as outer shelf or shelf basin deposits. They are more or less conformably overlain by white limestones of Danian age. Near the base there are two to three 'pebbly conglomeratic' levels, followed by thick to medium-bedded strata with thin more marly joints. These then pass upwards into a more regularly alternating series of limestones and marls. *Jeronia* occurs in the conglomeratic beds along with *Echinocorys*, while *Coraster* is most common towards the top of the section.

The uppermost beds here contain numerous planktonic foraminifera. These appear very close to *Planorotalites pseudomenardii* (Bolli) and *Acarinina mckannai* (White), which indicate Zone P4 (early Late Palaeocene). The new arcestdid was found in the upper marly alternations together with *Coraster*.

Casas de Oraien. This locality is placed in the middle of a wooded area some 200 m north-west of the farm buildings forming the hamlet of Oraien, which lies close to the village of Larumbe. The outcrop exposes medium-bedded, gritty calcareous sandstones in which echinoids, fragments of crinoid stems and oysters are the most common macrofaunal elements. The microfauna includes disco-cyclinid foraminifera indicative of a Thanetian age. The heterogeneous nature and size of the clasts, the shallow-water nature of the fossils contained and the fact that most echinoids are found chaotically in 'nests', suggest that these beds represent debris flow deposits where eroded material has been transported into a deeper part of the basin.

Aristregui. The road-cutting 500 m north of the village of Aristregui exposes a calcareous unit delimited by sharp contacts with predominantly marly levels both under and over it. A basal medium-bedded calcareous unit is followed by an alternation of marly limestones and marls, sometimes sandy, in which several intraformational conglomeratic levels occur. These beds have been dated on the basis of their microfauna as late Danian to early Thanetian (ZB 3-6) (Plaziat *et al.*, 1975). Plaziat *et al.* recorded the presence of the echinoids *Coraster beneharnicus*, *C. cf. sphaericus*, *Echinocorys douvillei* and *Jeronia pyrenaica* from near the base.

FAUNAL CHANGES ACROSS THE CRETACEOUS – TERTIARY BOUNDARY

The Late Cretaceous echinoid faunas from the Santander, Basque and Navarra regions of Spain are clearly very different, and were living in very different environments. Does this have any influence on the intensity of extinction suffered at the K-T boundary event?

Faunal diversity and water-depth. The faunas that we have studied come from three very different palaeoenvironments, and consequently have very different constituent species and overall diversities. The sequence at Santander was deposited in a shallow water (i.e. ca. 40–100 m) storm-disrupted, open-shelf environment. It contains by far the most diverse fauna (33 species), with most species coming from the shallowest facies (horizons 4 and 7/8). Not only is this habitat rich in species, but it is dominated by species of cassiduloid and regular echinoid. There are 12 regular echinoid, 9 cassiduloid, 3 holotrypoid, 6 holasteroid and 3 spatangoid species.

Virtually all of the species from the carbonate platform deposits of Olagazutia are also present at Santander, but at Olagazutia fewer taxa have been recorded. These beds were probably deposited at a similar water depth, but in a more sheltered setting, with less disturbance and less clastic influx. There are just nine species from Olagazutia. This may be in part a sampling artifact (smaller outcrop area), but the paucity of regular echinoids and cassiduloids suggests that the low diversity here may be genuine and reflect a lack of shallow-water elements.

The fauna of Santander is most similar to that described from the Limburg region around Maastricht, where comparable shallow-water deposits are found. 15 out of the 27 named species and 19 out of the 26 genera recorded at Santander also occur in the Maastricht district. The genera that appear at Santander, but which are not represented in Limburg, fall into two categories. First, there are shallow-water taxa, such as *Zuffardia*, *Clypeolampas* and *Acanthechinus*, whose distribution is primarily Tethyan, and secondly there are rare holasteroids (*Offaster* and *Galeaster*) that were primarily living in deeper-water settings and presumably near the shallow end of their range at Santander.

The shelf-basinal facies in Navarra, represented by black shale deposits, has, by comparison, a much less diverse fauna. These beds were deposited below storm wave-base, but were probably not particularly deep. They lie distal to a carbonate platform and were presumably more nutrient starved. The fauna of just six species is strikingly different to that of Santander, and only holasteroids and spatangoids are present. *Stegaster* is dominant in this environment, but not to the exclusion of other taxa.

In the truly deep-water, upper continental slope deposits of the Bidart region stegasterids (*Stegaster* and *Tholaster*) are the only echinoids present. This fauna is found elsewhere in deep-water chalks and shales from south eastern Spain, Turkey and North Africa, but is very different from the shelf chalk faunas that are found in northern Germany and Denmark. Stegasterids were specialist surface phytodetritivores.

There was thus a very clear depth control on both the diversity and composition of echinoid faunas in the late Cretaceous ocean. Shallow water faunas have high diversity, with a major component of bulk sediment feeding cassiduloids and algivorous regular echinoids. In environments below storm wave base atelostomates totally dominate and in really deep-water settings only stegasterid holasteroids, a group specialized as surface phytodetritus harvesters, existed.

Extinction levels. During the last stage of the Cretaceous 37% of echinoid genera became extinct (Jeffery & Smith, 1997, Smith & Jeffery, 1998). However, it is almost impossible to determine whether these extinctions were synchronous and instantaneous or sporadic and spread over thousands or millions of years. This is because of the serendipitous nature of the fossil record and because high resolution correlation is rarely possible in facies where echinoids are most abundant, due to the paucity of planktonic foraminifera or other biostratigraphically useful fossils. Even where we do have excellent stratigraphic control and continuous sections up to the Maastrichtian

– Danian boundary, as in the Basque region (Ward & Kennedy, 1993), the raw distribution pattern of taxa can be very misleading (Marshall & Ward, 1996, Jablonski, 1996, 1997). This is in part due to sampling artefact (e.g. the Signor-Lipps effect), whereby synchronous extinction events can appear gradual due to backward smearing of last records. However, changes in facies over time can also generate misleading patterns, with local disappearance being mistaken for global extinction as organisms migrate across the shelf tracking facies shifts driven by sea-level change. For example, although *Stegaster cotteai* appears to survive to within 40 m of the K-T boundary and then go extinct, this is not necessarily a correct interpretation for two reasons. Firstly, the sporadic occurrence of this species in the section suggests that, with more extensive sampling we might expect its true last appearance to lie closer to the K-T boundary. More importantly, the sister species to *S. cotteai* is *Sanchezaster habanensis* Lambert, a species known from the Lower Eocene of Cuba. Therefore, the lineage must have survived the K-T boundary event somewhere in the world even though it may have become locally extinct in the Biscay region.

Extinction levels at different water depths. A total of 40 Maastrichtian, nine Danian and nine Thanetian species are recognized in this work, the majority coming from shelf platform settings (within fair-weather wave base). Just three species from the Maastrichtian shallow water fauna are known from post-Maastrichtian deposits elsewhere, while only one of six species in basinal mudstones survives and none of the continental slope species has a post-Maastrichtian record. A literal reading of the fossil record would therefore suggest that there was 90% extinction at species level.

However, sea-level changes occurring at this time resulted in major changes in the distribution of sedimentary facies across Europe. For example, no shallow water faunas of Danian age are known from Spain, carbonate platform faunas reappearing only in the late Thanetian of the Pyrenees. Clearly this creates a major sampling bias that needs to be taken into consideration when attempting to assess levels of species extinction across the Cretaceous-Tertiary boundary. For that reason survivorship of higher clades (at generic level) is likely to give a more accurate picture. Maastrichtian species that belong to genera that have no post-Maastrichtian record can be assumed to have become extinct at around the K-T boundary, whereas those with post-Maastrichtian sister groups must clearly have passed through the interval.

Of the 25 Maastrichtian shallow-water genera reported here (see Appendix), 15 are known to survive into the Tertiary (a survivorship of 60%). For comparison three of the five shelf-basinal genera survive (60%) and one of the two continental slope genera survive (50%). Two of the three surviving genera (*Cyclaster* and *Echinocorys*) in the shelf basinal environments also occur in shallow-water faunas. If these are discounted, then we have 57% survival (13 out of 23 genera) of strictly shallow-water genera, and 25% (1 out of 4 genera) of strictly deeper-water genera.

Our sparse data therefore points towards extinction being rather more intense in shelf-basinal and upper slope settings, although the small numbers make any statistical testing meaningless. The demise of the deep-water fauna is probably linked to the plankton crash known to have occurred at the end Cretaceous, since the echinoids that become extinct are all specialist deposit feeders reliant on phytodetritus. The extinction in shallow platform settings is more difficult to assess, though here again food supply may have been crucial.

Extinction levels and palaeolatitude. Some workers (e.g., Macleod

& Keller, 1994) have suggested that faunas living at high latitudes may have suffered less extinction. So, how does the pattern of extinction and survival in Spain compare with that seen at other latitudes?

At the end Cretaceous northern Spain lay at approximately 35°N palaeolatitude (based on the palaeogeographic reconstruction of Scotese *et al.*, 1989). Two other late Cretaceous echinoid faunas, lying more or less at the same palaeolongitude, have been thoroughly documented from western Europe – from the Danish basin and from the Benelux area. The Maastrichtian of the Danish basin is composed of mid-shelf chalks best exposed on the islands of Zealand, Denmark, and Rügen, North Germany. Both lay at approximately 48°N palaeolatitude. In this basin changes in lithofacies do occur across the K-T boundary, but are much less pronounced than in any other part of Europe. As a result chalk facies occur in both the Maastrichtian and Palaeocene. Thirty-six Maastrichtian echinoid species are known, of which ten (28%) survive into the Danian. At generic level 18 of the 24 Maastrichtian genera found in Denmark (75%) have a post-Maastrichtian record.

The Maastrichtian of the Benelux region includes the type Maastrichtian from the Maastricht district and the richly fossiliferous Ciply deposits. This region lay at approximately 45°N palaeolatitude. The Early Maastrichtian is represented by mid-shelf chalks and shale-limestone facies while the Late Maastrichtian is predominantly composed of shallower carbonate platform facies. The Danian echinoids from the Guelhem Formation are rather unusual, being in a calcarenitic chalk facies, but dominated by distinctly shallow-water species. No Palaeocene facies comparable to the bioclastic limestones of the Maastricht Formation are found in this region. There are 54 Maastrichtian echinoid species recorded from this region (Smith & Jeffery, in press; Appendix), of which 11 continue directly into the Danian (20%). At generic level 28 of the 38 genera have a post-Maastrichtian record (74%).

If we include the Maastrichtian faunas of the eastern Pyrenees and the Alicante-Valencia basin with those described in this paper we have a total of 59 species and 43 genera from shallow, mid-shelf and deep-water settings at approximately 35° palaeolatitude. Sixteen of the 59 species (27%) and 27 of the 43 genera (63%) have a post-Maastrichtian record.

Extinction levels at all three palaeolatitudes are very similar, and survivorship at palaeolatitudes of 35° and 45–48° are not significantly different (χ^2 test $p > 0.90$) at both generic and species level. Therefore, across Europe there was no strong latitudinal gradient to end Cretaceous extinctions in echinoids.

Changes in faunal range. Maastrichtian genera that survive into the Palaeocene either continued in the same region or became locally extinct but survived elsewhere. The relative proportion of resident to emigrating lineages in an area reflects the degree to which local facies have been disrupted. If there is a significant change in facies then one might expect to see a high degree of local extinction at species level, but with many of the lineages (represented by congeneric species) continuing into the Palaeocene. Conversely, Palaeocene genera in each region can either represent resident lineages that have survived in the area, or immigrant lineages that appear in the area for the first time.

The fauna of the early Danian Geulhem Member of the Maastricht district described by Van der Ham (1988) is a striking example of how echinoid faunal ranges underwent a major reorganization after the K-T event. The Geulhem Member has just as diverse an echinoid fauna as any member of the Maastrichtian Maastricht Formation, but there are almost no species and very few genera in common between the two. A number of taxa known from the Maastrichtian of North

Africa or Spain (e.g., *Gitolampas*, *Circopeltis*, *Thylechinus*, *Linthia*) appear for the first time in the Guelhem Member. Conversely, there are also a large number of genera, present in the Maastrichtian of the Maastricht area, that are found only outside that area in the Palaeocene. Clearly there was a major shift in geographical ranges at the end Cretaceous.

Faunal immigration and emigration at the end of the Cretaceous is not restricted to the Benelux region. The Appendix gives a breakdown of the composition of the surviving Maastrichtian and Palaeocene genera in terms of their geographic origin. Only approximately one-third of taxa remained resident during this period, while significant immigration and emigration from all three regions discussed above took place (Table 2). The resulting pattern of high levels of local species extinction accompanied by marked shifts in generic range appears to characterize this time interval.

Table 2 Survivorship and migration data on western European echinoid genera at the end Cretaceous. See text for explanation.

	Generic survival	Palaeocene immigrants	Resident	Maastrichtian emigrants
Denmark basin	75%	9	10	8
Benelux area	74%	7	13	15
Spain	63%	15	12	15

SYSTEMATIC DESCRIPTIONS (A.B. Smith, J. Gallemí and C.H. Jeffery)

Order CIDADARIDA Claus, 1880

DIAGNOSIS. Regular echinoids with simple ambulacral plating and a single large primary tubercle on each interambulacral plate.

Family PSYCHOCIDARIDAE Ikeda, 1936

Genus TYLOCIDARIS Pomel, 1883

DIAGNOSIS. Primary tubercles imperforate, non-crenulate. Peristomial membrane contains ambulacral plates only. Primary spines clavate.

Tylocidar (*Sardocidar*) *ramondi* (Leymerie, 1851)

Pl. 1, fig. 1

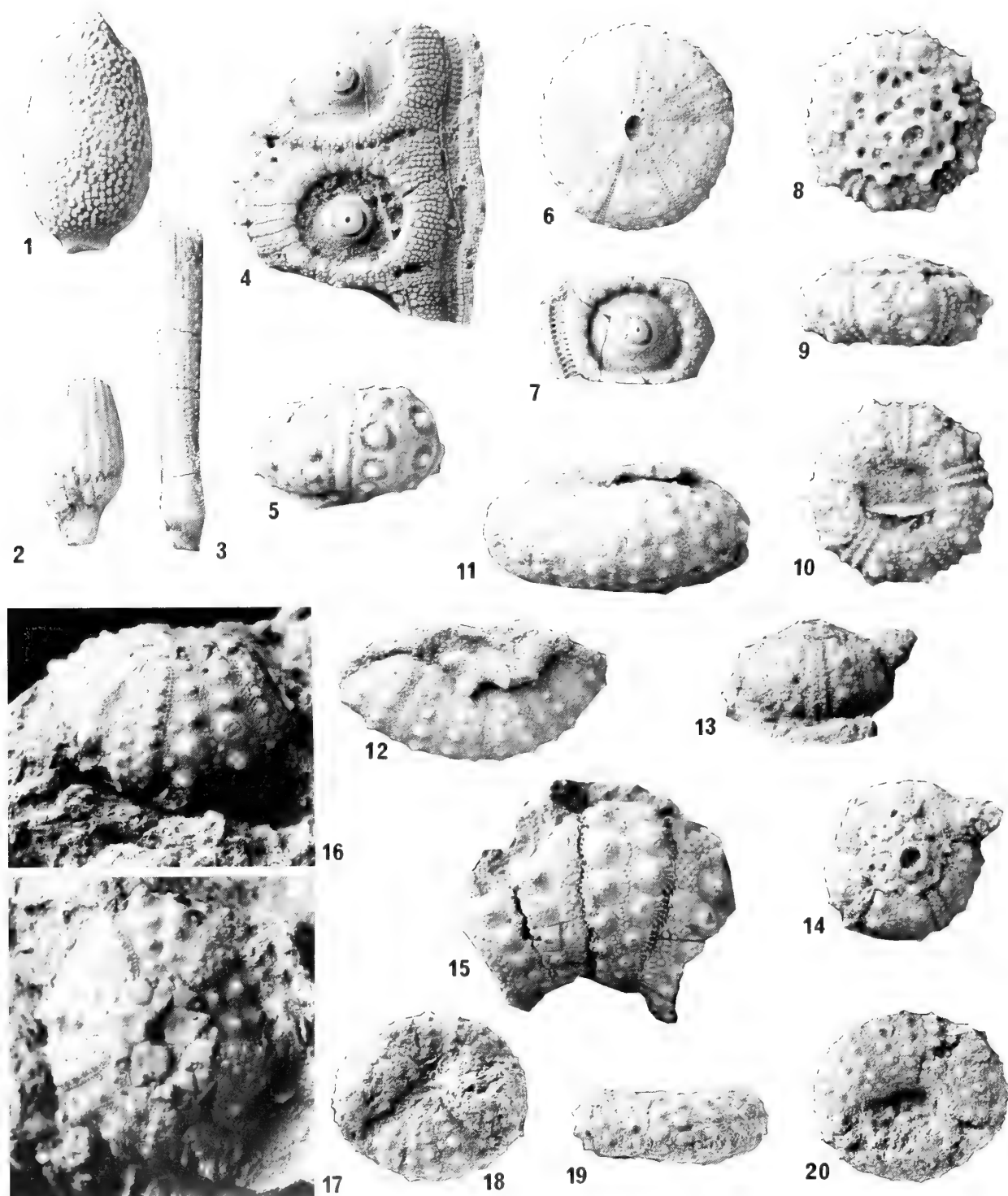
1851 *Cidar* *ramondi* Leymerie: 192, pl. 9, fig. 12 a, b, ?11c, d.

1857 *Cidar* *ramondi* Leymerie; Desor: 16, pl. 6, fig. 13.

1862a *Cidar* *ramondi* Leymerie; Cotteau: 315 (pars), pl. 1076, figs 1–8, 10–12, 14–17.

1910 *Tylocidar* *ramondi* (Leymerie); Lambert & Thiéry: 156.

DIAGNOSIS. Test large with more than seven interambulacral plates in a column (as opposed to the five typical of *Tylocidar* (*Tylocidar*)). Ambulacra broad, with contiguous outer series of primary tubercles and inner series of three or four smaller granules in two irregular rows on each plate. Spines large, up to 25 mm in length, with a highly characteristic bulbous shaft, short neck and sharp transition to shaft. Shaft widest one-quarter of the distance above the base; width 50–60% of length. Distal end of spine bluntly pointed. Surface densely covered in coarse granules that are more or less contiguous, leaving no intergranular spaces. Granules are generally



randomly arranged, but occasionally form longitudinal lines near the distal tip.

MATERIAL STUDIED. BMNH EE4545a–h, EE6265–68, MGB 37444–49, 37480–87.

OCCURRENCE. The species is based on tests and isolated spines from the Maastrichtian of Monléon and Gensac, Haute-Garonne, French Pyrenees. In Spain spines and isolated interambulacral plates are moderately common in the Maastrichtian, horizon 6, of Olazagutia Pass, Navarra province. Lambert (1907: 712) recorded this species from 'Garumnian facies' of Bouzin (Haute-Garonne, France) which is Danian in age. This, however, is based on a test and the characteristic spines of *T. ramondi* were not apparently collected. It is not therefore certain to what species this test should be assigned.

REMARKS. A readily distinguishable species of *Tylocidaris* on account of its characteristically shaped spines and slightly greater number of interambulacral plates. The spines are readily distinguishable from those of *Tylocidaris trempinus* in both shape and ornament. Whereas *T. ramondi* spines are fat, glandiform and rapidly taper to a blunt point distally, those of *T. trempinus* are more fusiform and distally elongate, tapering to a more distinct point. More importantly, the ornament on the shaft of *T. ramondi* consists of rather fine and dense granulation that is arranged irregularly, whereas in *T. trempinus* the ornament comprises rather stout and well-formed beaded ribs, from the neck to the distal tip.

***Tylocidaris (Sardocidaris) trempinus* Gallemí & Smith,**
sp. nov. Pl. 1, fig. 2

?1851 Spines of an unknown *Cidarid*, Leymerie: 192, pl. 9, fig. 13.

?1862a *Cidarid ramondi* Leymerie; Cotteau: 315 (pars), pl. 1076, figs 9, 13.

1920 *Tylocidaris ramondi* Leymerie; Lambert: 4.

1992 *Sardocidaris ramondi* (Leymerie); Gallemí: 56, photo 4.

DIAGNOSIS. Spines up to 28 mm in length, fusiform, with widest part of shaft about one-third above the base. Shaft tapering to a small blunt point distally and also tapering towards the base; width less than one-third of length. No distinct handle is developed beneath the shaft. The entire shaft is ornamented with relatively stout beaded ribs, densely spaced. Base imperforate and non-crenulate.

TYPES. Holotype Universitat Autònoma de Barcelona, Palaeontological Collections PUAB-4321 illustrated by Gallemí (1977: 11, pl. 1, fig. 3); paratypes PUAB-4055 (*op. cit.* pl. 1, fig. 4) and PUAB-43626–32.

OTHER MATERIAL STUDIED. BMNH EE6114–15, MGB 37513, 37514, 37545.

OCCURRENCE. In Spain this species occurs in the Upper Campanian of Toralla, near La Pobla de Segur, Tremp Basin and Lower Maastrichtian, Serra dels Homes Morts (Salàs de Pallars) and Orcau, Tremp Basin (Gallemí, 1992). It also occurs in the Maastrichtian, horizons 4 and 6, at Santander.

REMARKS. Differs from spines of *T. ramondi* in having an ornament of continuous beaded ribs instead of dense irregular granulation. Differs from spines of *Tylocidaris clavigera* (Mantell), *T. inexpectata* Jagt & Van der Ham and *T. hemmoorensis* Salah & Schmid in its strongly fusiform and distally tapering shape. Spines of *T. baltica* are more bulbous and have only fine irregular granulation. Leymerie (1851) reported finding very occasional spines in the Maastrichtian of Monléon and Gensac, Haute-Garonne, French Pyrenees that were clearly different from those of *T. ramondi*. Although he did not name these, they appear to match those from Tremp.

***Tylocidaris* sp.** Pl. 1, fig. 5

DIAGNOSIS. Small test approximately 17 mm in diameter and 9.3 mm in height. Peristome and apical disc similar in size, approximately 5.5–6 mm in diameter. Interambulacral zones wide with primary tubercles offset towards adradial margins. Primary tubercles imperforate, noncrenulate. Six plates in each column. Ambulacra weakly sinuous with primary tubercles to each plate and perradial granulation.

MATERIAL STUDIED. BMNH EE6109.

OCCURRENCE. Maastrichtian, horizon 2, of Santander, Cantabria.

REMARKS. The various species of *Tylocidaris* all have very similar test morphology. Without associated spines it is virtually impossible to determine such material to species level.

Family **CIDARIDAE** Gray, 1825

Genus **TEMNOCIDARIS** Cotteau, 1863

DIAGNOSIS. *Cidaroids* with perforate, non-crenulate tubercles; some fully formed adapical plates with rudimentary tubercles. Ambulacral pores non-conjugate.

***Temnocidaris (Temnocidaris) magnifica* Cotteau, 1863**
Pl. 1, figs 3, 4

1863a *Temnocidaris magnifica* Cotteau: 357, pl. 1085, 1086.

PLATE 1

Fig. 1 *Tylocidaris (Sardocidaris) ramondi* (Leymerie, 1851), BMNH EE4545, Maastrichtian of Olazagutia Pass, Navarra. Spine, $\times 2$.

Fig. 2 *Tylocidaris (Sardocidaris) trempinus* sp. nov., BMNH EE6114, Maastrichtian of Santander, Cantabria. Spine, $\times 2$.

Figs 3, 4 *Temnocidaris (Temnocidaris) magnifica* Cotteau, 1863, Maastrichtian of Santander, Cantabria. **3**, BMNH EE4415, interambulacral plates and associated ambulacrum, $\times 2$; **4**, BMNH EE6111, spine, $\times 2$.

Fig. 5 *Tylocidaris* sp. BMNH EE6109, Maastrichtian of Santander, Cantabria. Test in profile, $\times 2$.

Fig. 6 *Orthopsis miliaris* (d'Archiac, 1835), BMNH EE6118, Maastrichtian of Santander, Cantabria. Apical view of test, $\times 1.5$.

Fig. 7 Indet. *cidarid*, BMNH EE6113, Maastrichtian of Santander, Cantabria. Interambulacral plate and associated ambulacral plates, $\times 2$.

Figs 8–10 *Salenia (Pleurosalenia) maestrichtensis* Schlüter, 1892, BMNH EE4423, Maastrichtian of Olazagutia Pass, Navarra. Apical, lateral and oral views, $\times 2$.

Figs 11, 12 *Acanthechinus* sp. BMNH EE6128, Maastrichtian of Santander, Cantabria. Lateral and apical views, $\times 2$.

Figs 13, 14 *Salenia (Pleurosalenia) scabra* (Nestler, 1965), BMNH EE6110, Maastrichtian of Santander, Cantabria. lateral and apical views, $\times 1.5$.

Fig. 15 *Phymosoma hexaporum* Lambert, 1927, MGB 37556, Maastrichtian of Santander, Cantabria. Adoral portion of test, $\times 2$.

Figs 16, 17 *Goniopygus tetraphyma* Lambert, 1907, BMNH EE4419, Maastrichtian of Santander, Cantabria. Lateral and apical views, $\times 2$.

Figs 18–20 *Gauthieria pseudomagnifica* (Cotteau, 1877), BMNH EE6117, Thanetian of Casas de Oraien, Navarra. Apical, lateral and oral views.

non1982 *Temnocidaris magnifica* Salah: 209, pl. 1, figs 1–3 [= *Stereocidaris serrata* Desor]

DIAGNOSIS. Large *Temnocidaris* with relatively fine extrascrobicular tuberculation, six abreast adradially and up to 16 abreast interrally; interambulacra with *ca.* seven plates in a column; plates almost twice as wide as tall, so that primary tubercles occupy virtually the entire plate height and scrobicular circles are tangential at the ambitus. Ambulacral plates with large primary tubercle, followed by one or two secondary tubercles and then more irregular perradial tuberculation in two rows. Pitting strongly developed both in ambulacra and in interambulacral extrascrobicular zones. Spines long, cylindrical with finely thorned ribs.

OCCURRENCE. Maastrichtian, horizons 2 and 7/8, of Santander. The species was first described from the Maastrichtian of Aurignac, Haute-Garonne, France, and is also known from Cotentin, south west France.

MATERIAL STUDIED. BMNH EE4415, EE6111.

REMARKS. This species is distinguished from the very closely related *T. danica* by its finer extrascrobicular granulation. In *T. magnifica* extrascrobicular granulation is about 67% the diameter of that in *T. danica*. Only isolated spines were found in beds at Santander which are tentatively assigned to this species because of their similarity to spines of other species of *T. (Temnocidaris)*.

Indet. cidarid plates

OCCURRENCE IN SPAIN. Maastrichtian, horizons 2, 4, 5, and 7/8 of Santander; Maastrichtian, horizon 6, of Olazagutia Pass.

REMARKS. Isolated cidaroid plates with perforate noncrenulate tubercles and narrow extrascrobicular tuberculation and belonging to at least two different taxa have been collected from the Maastrichtian of Santander and Olazagutia. This material is too fragmentary to place even to genus.

Cohort ECHINACEA Claus, 1876

DIAGNOSIS. Regular echinoids with keeled teeth and compound ambulacral plating.

Family ORTHOPSIDAE Duncan, 1889

Genus ORTHOPSIS Cotteau, 1864

DIAGNOSIS. Primary tubercles perforate and non-crenulate. Ambulacra trigeminate with acrosaleniid-style plate compounding.

Orthopsis miliaris (d'Archiac, 1835) Pl. 1, fig. 6

1835 *Cidarites miliaris* d'Archiac: 170, pl. 11, fig. 8.

1864a *Orthopsis miliaris* (d'Archiac); Cotteau, in Cotteau 1861a–67a: 558, pl. 1131, figs 1–16 (with full synonymies up to the date).

1895 *Orthopsis morgani* Cotteau & Gauthier: 87, pl. 14, figs 6–9.

1985 *Orthopsis miliaris* (d'Archiac); Geys: 134, pl. 5, figs 8–10.

1991 *Orthopsis miliaris* (d'Archiac); Smith & Bengtson: 30, text-fig. 23, pl. 8, figs B–F.

1995 *Orthopsis miliaris* (d'Archiac); Smith: 136, figs 12–14, pl. 2, figs 4–5; pl. 3, figs 1–9.

DIAGNOSIS. Test up to *ca.* 25 mm in diameter; depressed; rounded in profile with ambitus slightly below mid-height. Apical disc dicyclic;

usually preserved in position. Ambulacra straight with uniserial columns of pore-pairs. Plating trigeminate with all three elements reaching the perradial suture; primary tubercle overlapping two of the three elements only. Interambulacra with central primary tubercle and slightly smaller secondary tubercles on adradial and interrally margins from ambital region adorally. Peristome moderately large and slightly sunken.

OCCURRENCE IN SPAIN. Maastrichtian, horizons 7/8 and 9, of Santander; Upper Campanian of Barranc de Vilanova, Toralla, near La Pobla de Segur, Tremp Basin and Lower Maastrichtian of Homes Morts Member, Salàs de Pallars, Tremp Basin (Gallemí, 1992). This species is widely distributed in the Upper Cretaceous of Europe and the Middle East (Smith & Jeffery, in press).

MATERIAL STUDIED. MGB 37563, 37564, BMNH EE6118–24.

Order CALYCINA Gregory, 1900

DIAGNOSIS. Regular echinoids with stout elevated cap-like apical system that incorporates one or more large suranal plates firmly bound to the ring of genital plates.

Family SALENIIDAE Agassiz, 1838

Genus SALENIA Gray, 1835

DIAGNOSIS. Periproct offset towards ocular I.

Subgenus SALENIA (PLEUROSALÉNIA) Pomel, 1883

DIAGNOSIS. *Salenia* with predominantly simple ambulacral plating; plating entirely simple towards peristome.

Salenia (Pleurosalenia) scabra (Nestler, 1965)

Pl. 1, figs 13, 14; Fig. 6

1950 *Salenidia bonissenti* Cotteau; Kongiel: 311, 321, pl. 1, figs 1–4.

1965 *Salenidia scabra* Nestler: 987, pl. 4, figs 4–7.

1973 *Salenidia scabra* Kutscher: 111, figs 13, 14.

1975 *Salenidia scabra* Nestler: 89.

1979 *Salenidia* cf. *bonissenti* Cotteau; Geys: 890, pl. 1, fig. 4, pl. 2, fig. 2, pl. 3, figs 6–8, pl. 4, figs 1, 2.

1987 *Salenidia* ?*bonissenti* Van der Ham et al.: 21.

DIAGNOSIS. Up to 15 mm diameter; relatively tall (height *ca.* 60% test diameter). Apical disc subconical, weakly pentastellate in outline with ocular plates projecting slightly. Periproct small, trigonal, with slight lip. Large oval sutural pits at triple junctions and mid-length along all disc plate sutures; strong ridges run radially between the sutural pits giving the disc a very characteristic appearance. Ambulacra straight, unigeminate throughout (rare bigeminate elements at ambitus), with relatively wide perradial band of granulation separating primary tubercles. Five interambulacral plates in a column.

OCCURRENCE. Maastrichtian of Santander, horizon 4. Elsewhere the species is known from the late Early Maastrichtian of Rügen, Germany, Late Maastrichtian of Poland and Eben-Emael, Belgium.

MATERIAL STUDIED. BMNH EE4423a, b, BMNH EE4430, MGB 37575.

REMARKS. Separated from *S. anthophora* at comparable test diameters by having a smaller sized disc. *Salenia bonissenti* (Cotteau,

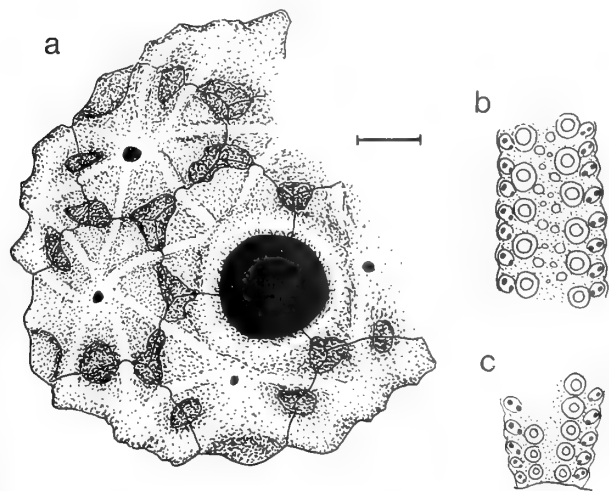


Fig. 6 Camera lucida drawings of plating in *Salenia* (*Pleurosalenia*) *scabra* (Nestler, 1965) from the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6110. **a.** apical disc; **b.** adapical ambulacrum; **c.** adoral ambulacrum, peristome at base. Scale bar = 1 mm.

1866b) has usually been treated as a distinct species characterized by having sharp carina on apical disc plates (e.g. Geys, 1979). However, Cotteau's original illustrations do not show sharp carina, only a somewhat gentle undulose plate surfaces similar to many specimens of *S. anthophora*. The oldest available name for forms with sharp carina radially arranged on genital and suranal plates is *Salenidia scabra* Nestler (1965).

***Salenia* (*Pleurosalenia*) *maastrichtensis* Schlüter, 1892**
Pl. 1, figs 8–10

- 1857 *Salenia bourgeoisi* Bosquet: 3.
1862 *Salenia bourgeoisi* Cotteau, in Cotteau 1861a–67a: 162 (pars), pl. 1040, figs 25–28.
1892 *Salenia Maastrichtensis* Schlüter: 196.
1935 *Salenia bourgeoisi* Cotteau; Smiser: 26, pl. 2, fig. 7.
1979 *Salenidia maastrichtensis* Schlüter; Geys: 298, figs 1.1–1.7.
1979 *Salenidia sanctipetri* Geys: 303, figs 5.1–5.6, 6.1–6.2.
1987 *Salenidia maastrichtensis* Schlüter; Van der Ham *et al.*: 21, pl. 2, fig. 3.
1987 *Salenidia sanctipetri* Geys; Van der Ham *et al.*: 22.

DIAGNOSIS. Test generally rather small (up to about 12 mm test diameter), and depressed in profile (height ca. 50% of test diameter). Apical disc flat with raised margins and a small but distinct rim surrounding the periproct. Periproct in general rather small, slightly smaller than the suranal plate. Ocular plates T-shaped, projecting beyond genital plates slightly. Sutural pits large, present at all triple junctions and in addition midway along genital-ocular plate sutures; becoming quite angular in large individuals. Ambulacra straight and relatively wide, with outer columns of contiguous primary tubercles and an inner band of secondary tubercles with intervening granules. Rare bigeminate elements may be present, but for the most part ambulacra are unigeminate. Interambulacra wide with primary tubercles positioned close to the adradial, leaving a broad, somewhat depressed interradiar zone of secondary granules. Primary tubercles with relatively coarse mamelons. Peristome small and somewhat invaginated.

OCCURRENCE. Spanish material comes from the Maastrichtian, horizon 6, Olazagutia Pass, Navarra province and Maastrichtian, horizon 4, Santander. The species was first described from the Late Maastrichtian Chalk of the Maastricht district, The Netherlands and Belgium, and is also reported from the Ciply Craie phosphatée and St Symphorien Gravel at Ciply, Belgium (*vide* Geys, 1979).

MATERIAL STUDIED. BMNH EE4423a, b, EE4430, MGB 37574.

REMARKS. The distinction between this species and juvenile *S. anthophora* is difficult. In both species apical disc plates are characteristically dimpled at small sizes, and it may be that the two forms cannot be separated until test sizes of about 1 cm have been reached. By this size *S. maastrichtensis* is obviously flatter and has wider and more depressed interradiar bands than *S. anthophora*.

Subgenus *SALENIA* (*SALENIA*) Gray, 1835

DIAGNOSIS. *Salenia* with predominantly bigeminate ambulacral plating; plating never simple adorally.

***Salenia* (*Salenia*) sp.**

DIAGNOSIS. A small individual 4.2 mm in diameter with a large apical disc with prominent sutural pits. Ambulacral plating bigeminate at ambitus and adorally.

MATERIAL STUDIED. BMNH EE4431.

OCCURRENCE. Maastrichtian, horizon 9, Santander.

REMARKS. This specimen is clearly distinct from the other saleniids described here on account of its bigeminate ambulacral plating. However, it is too small an individual to identify with confidence to species level.

Order ARBACIOIDA Gregory, 1900
Family GONIOPYGIDAE Smith & Wright, 1993
Genus GONIOPYGUS Agassiz, 1838

DIAGNOSIS. Apical disc solid and raised above the corona; no suranal plate present; genital plates pointed with gonopore opening at tip or in immediately adjacent interambulacra. Primary tubercles imperforate, non-crenulate. Ambulacral plating basically trigeminate with upper element in each triad occluded.

***Goniopygus tetraphyma* Lambert, 1907 Pl. 1, figs 16, 17**

- 1907 *Goniopygus tetraphyma* Lambert: 701, pl. 25, figs 7–9.
1949 *Goniopygus jeanneti* Sánchez Roig: 54, pl. 2, figs 7, 8.

DIAGNOSIS. Test up to 25 mm diameter; subconical in profile with low ambitus and small flat summit. Apical disc solid, elevated above the corona; dicyclic, with pointed genital plates; gonopores opening at the very distal point of genital plates, beyond the elevated portion. Periproct small, trigonal, with three perianal tubercles. Ambulacra wide, trigeminate throughout with small phyllodes adorally; each plate carrying a large primary tubercle and a smaller secondary tubercle, the latter forming a distinct inner series. Interambulacra with single large primary tubercle; adapical plates lacking secondary tubercles, but those from the ambital region adorally have five or six small secondary tubercles. Peristome large, hardly sunken.

OCCURRENCE. Maastrichtian, horizon 7/8, Santander. The type of this species comes from the Upper Cretaceous of Roquefort (Haute-

Garonne, France). It is also known from the Upper Cretaceous of Cuba and from the Maastrichtian of Fígols, Llobregat River basin, Catalonia, Spain (MGB collections).

MATERIAL STUDIED. BMNH EE4419, EE6129, MGB 37576.

REMARKS. Easily distinguished from other species of *Goniopygus* by its very wide ambulacra with prominent double columns of secondary tubercles. Only the 25 mm diameter individual shows the distinct double ambulacral tubercles characteristic of this species. Two very much smaller specimens (less than 10 mm) from the same horizon are tentatively assigned to this species, although they are too small to have developed prominent secondary ambulacral tuberculation.

Order **PHYMOSOMATOIDA** Mortensen, 1904

Family **PHYMOSOMATIDAE** Pomel, 1883

DIAGNOSIS. Apical disc not firmly bound to corona; large and monocyclic, but plating usually lost. Ambulacra polygeminate with phymosomatid-style compounding. Primary tubercles imperforate and crenulate.

Genus **GAUTHIERIA** Lambert, 1888

DIAGNOSIS. Phymosomatids with pore-pairs uniserial throughout. One large interambulacral tubercle on ambital interambulacral plates with small adradial tubercles present on adoral plates. Peristome usually deeply sunken.

Gauthieria pseudomagnifica (Cotteau, 1877)

Pl. 1, figs 18–20

1863 *Cyphosoma magnificum* Cotteau: 185 (*nomen nudum*).

1877 *Cyphosoma pseudomagnificum* Cotteau; Cotteau: 55, pl. 4, figs 1–6.

DIAGNOSIS. Test up to 35 mm in diameter; circular in outline and depressed in profile (height about 40–50% of diameter). Apical disc opening pentagonal, relatively small (30% of test diameter). Peristome equally small and deeply invaginated. Ambulacra tapering adapically; ambital compound plate with six or seven pore-pairs defining weak arcs; pore-pairs remain uniserial throughout, with no pore-crowding adorally. Single large primary tubercle on each ambulacral and interambulacral plate. Tubercles large with circular areole and relatively small mamelons. Much smaller secondary tubercles present on adradial and interradian margins of subambital plates. Granulation outside primary tubercles rather poorly devel-

oped. Distinct interradian naked zone developed adapically.

OCCURRENCE. Our two specimens come from the Upper Thanetian, *P. pseudomenardii* Zone, limestone of Casas de Oraien, near Larumbe, Navarra, Spain. The type locality for this species is the Thanetian of Belbèze, Haute-Garonne, France. It has also been recorded from the Thanetian of Le Tuco near Cazeneuve, Haute-Garonne, France, and from the Petites Pyrénées (Plaziat *et al.*, 1975).

MATERIAL STUDIED. BMNH EE 6117, MGB 37425.

REMARKS. The arcuate uniserial arrangement of ambulacral pore-pairs distinguish this species from other phymosomatid species described here.

Genus **DIPLOTAGMA** Schlüter, 1870

DIAGNOSIS. Phymosomatid with biserial pore-pairs developed from the ambitus adapically and with strong adoral phyllodes. Test subconical and apical disc rather small. Interambulacral plates very wide and low with primary tubercles contiguous in column; broad granular zones developed both interradianly and perradianly. Tubercles imperforate and crenulate.

Diplotagma sp.

Pl. 2, figs 1, 2

DIAGNOSIS. Test 37–38 mm in diameter and about 23 mm in height. Apical disc about 50% of test diameter, peristome slightly larger and a little sunken. Pore-pairs arranged biserially from the ambitus adapically but in arcs subambitally and forming phyllodes adorally. Subambital plates have five pore-pairs to a plate, adapical plates with four pore-pairs. Ambulacral tubercles are contiguous in vertical columns and are separated by a wide perradian zone of granulation. Interambulacral plates are very wide (more than three times broader than tall at the ambitus) and have a single primary tubercle. Secondary tubercles are developed adradially, one on oral plates and up to three on ambital and supra-ambital plates.

OCCURRENCE. Maastrichtian, horizon 7/8, Santander.

MATERIAL STUDIED. BMNH EE4417.

REMARKS. Our only specimen is rather badly abraded, but shows the general features of *Diplotagma*, namely the rather delicate primary tubercles and broad granular adradial and interradian zones, together with the biserially arranged pore-pairs from the ambitus to the apex. Its strongly developed adoral phyllodes distinguishes it from *Acanthechinus*. *Diplotagma* sp. nov. (Smith & Jeffery, in press), from the Upper Maastrichtian of the Maastricht area, differs from the Spanish specimen in having narrower, coarser and more heterogeneous interradian tuberculation.

PLATE 2

Figs 1, 2 *Diplotagma* sp., BMNH EE4417, Maastrichtian of Santander, Cantabria. Oral and aboral views, $\times 1.5$.

Figs 3, 4 *Phymosoma granulosum* (Goldfuss, 1829), BMNH EE6127, Maastrichtian of Santander, Cantabria. Apical and lateral views, $\times 2$.

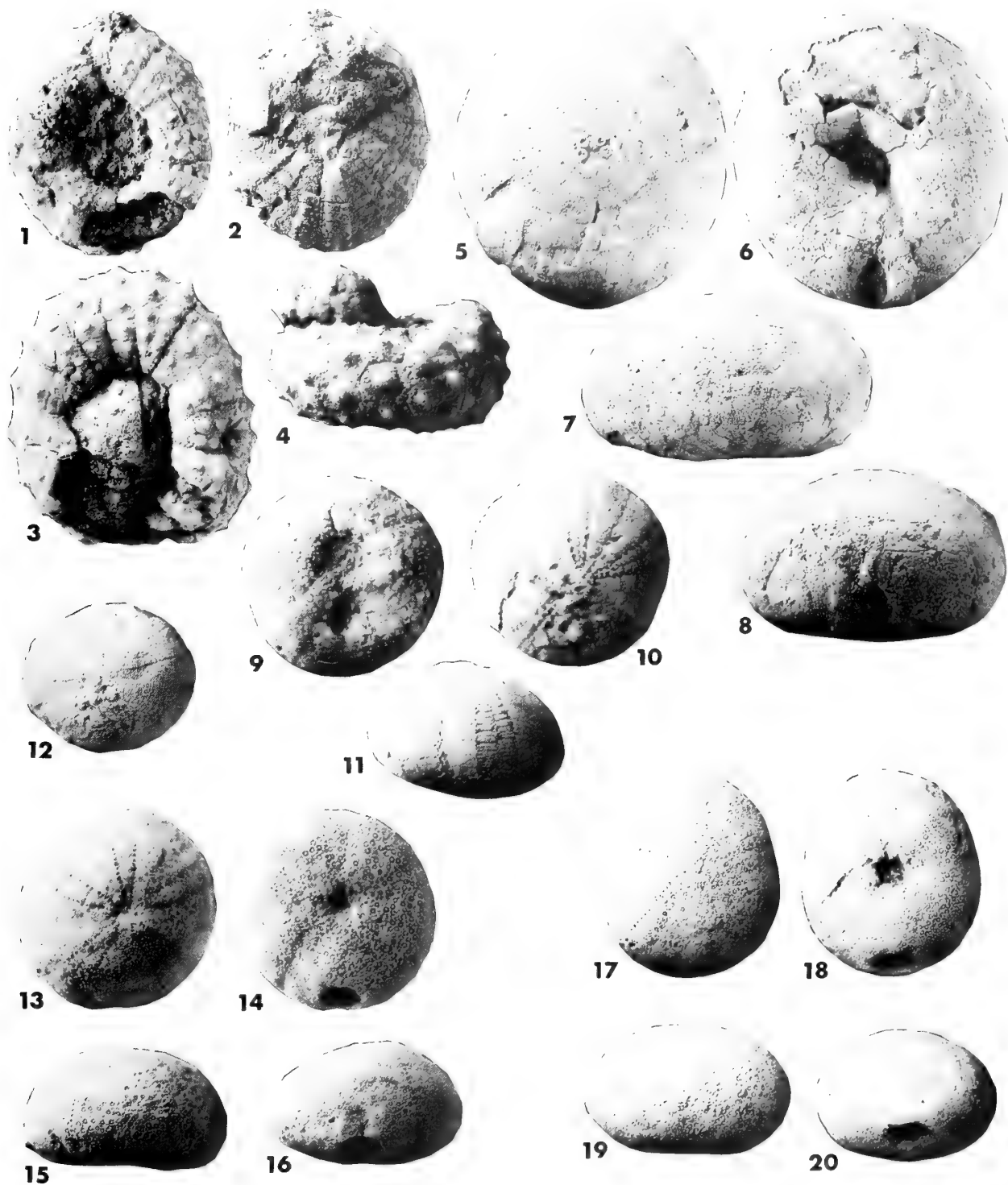
Figs 5–8 *Adelopneustes ernstii* Smith & Gallelli, BMNH EE6134 (**holotype**), Thanetian of Casas de Oraien, Navarra. Apical, oral, lateral and posterior views, $\times 2$.

Figs 9–11 *Camerogalerus cantabricus* Smith & Gallelli, BMNH EE6132 (**holotype**), Maastrichtian of Santander, Cantabria. Oral, apical and lateral views, $\times 5$.

Fig. 12 *Coenholectypus noctigali* (Krumbeck, 1906), BMNH EE6129, Maastrichtian of Santander, Cantabria. Apical view, $\times 1.5$.

Figs 13–16 *Echinogalerus vetschauensis* (Schlüter, 1902), BMNH EE6164, Maastrichtian of Santander, Cantabria. Apical, oral, lateral and posterior views, $\times 3$.

Figs 17–20 *Echinogalerus muelleri* (Schlüter, 1902), BMNH EE6138, Maastrichtian of Olagazutia Pass, Navarra. Apical, oral, lateral and posterior views, $\times 3$.



Genus *PHYMOSOMA* Haime, in d'Archiac & Haime, 1853

DIAGNOSIS. Test depressed with apical disc opening large and peristome hardly invaginated. Pore-pairs forming short phyllodes adorally and becoming biserial adapically. Primary tubercles relatively coarse, occupying most of the interambulacral plate. Tubercles imperforate and crenulate.

Phymosoma granulosum (Goldfuss, 1829) Pl. 2, figs 3, 4

1829 *Cidarites granulosus* Goldfuss: 122, pl. 40, fig. 7.

1865 *Cyphosoma granulosum* Cotteau, in Cotteau 1861a–67a: 684, pl. 1169.

1898b *Gauthieria broeki* Lambert: 152, pl. 4, figs 1–5.

DIAGNOSIS. Test 20–25 mm in diameter, depressed in profile with rounded ambitus. Ambulacra with five-geminate plate compounding; pore-pairs arranged in arcs on ambital plates but becoming biserial towards the apex. Large primary tubercle on ambulacral plates, separated by single band of granules on ambital plates. Short phyllodes developed adorally. Interambulacral plates a little wider than tall and dominated by a single large primary tubercle with a large mamelon. Narrow adradial and interrarial bands. Peristome hardly invaginated.

OCCURRENCE. Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6127.

REMARKS. Distinguished from *Diplotagma* sp. by its relatively coarse interambulacral tuberculation, the tubercles largely filling each interambulacral plate. Distinguished from *Acanthechinus* sp. in having its peristome hardly invaginated and in having obvious adoral phyllodes. *P. hexaporum* is similar, but has more pore-pairs to each ambital ambulacral plate (six or seven as opposed to five) and has distinct secondary tubercles to the adradial side of primary tubercles on ambital and supraambital plates.

Phymosoma hexaporum Lambert, 1927
Pl. 1, fig. 15; Fig. 7

1927 *Phymosoma hexaporum* Lambert: 35, pl. 2, figs 25–27.

1928 *Phymosoma hexaporum* Lambert: 61.

1992 *Phymosoma hexaporum* Gallemí: 80, fig. 24.

DIAGNOSIS. Test relatively large and depressed, up to about 40 mm diameter (estimated). Apical disc pentagonal, peristome slightly sunken and small (about 12 mm, estimated). Ambulacral plates occupied by single large primary tubercle; areoles confluent adorally and just separated on ambital and aboral plates. Pore-pairs in arcs of six on ambital and subambital plates and forming distinct phyllodes adorally. Aboral pore-pairs presumably arranged biserially, as in the type, although none of our specimens has a well-preserved upper surface. Granulation rather sparse. Interambulacral plates distinctly wider than tall with adradial and interrarial granular zones. Small secondary tubercles only very weakly differentiated adradially on adoral and subambital plates, but better developed adapically.

OCCURRENCE. Maastrichtian, horizons 4 and ?7/8, Santander. Campanian/Maastrichtian beds at Erice, Navarra.

MATERIAL STUDIED. MGB 37556, BMNH EE6126, EE4422, ?EE4416.

REMARKS. Distinguished from *Diplotagma* by its taller interambulacral plates and stouter primary tubercles, and by its uniserially arranged pore-pairs on ambital plates. It differs from *P. granulosum*

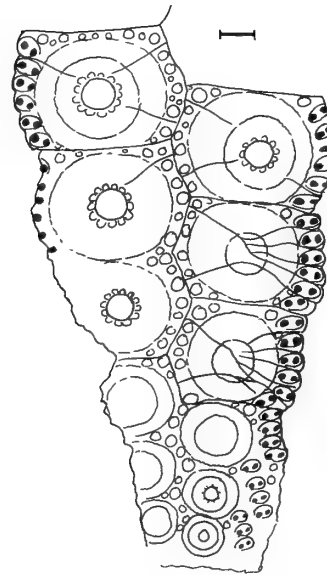


Fig. 7 Camera lucida drawing of plating in *Phymosoma hexaporum* Lambert, 1927 from the coast west of Cabo Mayor (Santander, Cantabria); MGB 37556, adoral part of an ambulacrum. Scale bar = 1 mm.

in having wide zones of granulation and by having six or seven rather than five pore-pairs to each ambital ambulacral plate.

Genus *ACANTHECHINUS* Duncan & Sladen, 1882

DIAGNOSIS. Phymosomatid with pore-pairs arranged biserially from the ambitus aborally. Peristome deeply invaginated and pore-pairs arranged uniserially adorally without phyllodes; primary ambulacral tubercles not crowded adorally. One large primary tubercle to each interambulacral plate.

Acanthechinus sp. Pl. 1, figs 11, 12

DIAGNOSIS. Specimen between 25 and 28 mm diameter; height 9.3 mm; rounded in profile with ambitus a little below mid-height. Apical disc moderately large; peristome smaller, strongly invaginated. Ambulacra tapering adapically; pore-pairs uniserial below the ambitus but biserial from the ambitus adapically. Six or seven pore-pairs to an aboral plate, but five on ambital plates. Ambulacral plates with single large primary tubercle; tubercles separated by a single row of granules both perradially and within a single column. Tubercles remain separated towards the peristome. Eleven interambulacral plates in a column, each with a single primary tubercle. Plates wider than tall and primary tubercles confluent on ambital and adoral plates. A band of small secondary tubercles is developed along the adradial plate margin on the oral surface. On plates just above the ambitus, a distinctly enlarged secondary tubercle appears close to the adradial margin.

OCCURRENCE. Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6128.

REMARKS. The deeply sunken peristome, and relatively small and wide plates, distinguish this from the two *Phymosoma* species. It resembles *Diplotagma*, but that species has shorter and wider interambulacral plates, with wider and more granular interrarial and perradial bands. Furthermore, *Acanthechinus* has a deeply sunken

peristome, whereas in *Diplotagma* the peristome is hardly sunken and there are well-developed phyllodes. Lambert (1907) described a species of *Acanthechinus*, *A. savigni* (as *Phymosoma*), from the Maastrichtian of Gensac, Haute-Garonne, France. This is based on a single large individual 56 mm in diameter. This specimen has seven pore-pairs to an ambital ambulacral plate, whereas our specimen has just five. For this reason we are hesitant to unite the two. However, the number of pore-pairs associated with ambital plates does increase during growth in the closely related *A. spectabile* Cotteau & Gauthier, from the Maastrichtian of the United Arab Emirates (Smith 1995), and it is possible that the two are conspecific. More material from both populations is required, however.

Cohort **IRREGULARIA** Latreille, 1825

DIAGNOSIS. Periproct opens outside the apical disc circlet.

Order **HOLECTYPOIDA** Duncan, 1889 Family **HOLECTYPIDAE** Lambert, 1900

DIAGNOSIS. Pore-pairs undifferentiated in ambulacra. Peristome central, circular, with buccal notches.

Genus **COENHOLECTYPUS** Pomel, 1883

DIAGNOSIS. Holectypoids with five gonopores and test lacking internal buttressing.

Coenholectypus nactigali (Krumbeck, 1906) Pl. 2, fig. 12; Fig. 8d, e

- 1906 *Discoidea Nactigali* Krumbeck: 86, pl. 7.
1907 *Holectypus proximus* Lambert: 701, pl. 25, figs 12–14.
1977 *Coenholectypus proximus* Gallemí: 62, pl. 10.
1979 *Coenholectypus proximus* Gallemí: 356, pl. 1.
1992 *Coenholectypus proximus* Gallemí: 124, figs 37, 38.

DIAGNOSIS. Test small, up to 15 mm diameter; depressed, with ambitus relatively low; lower surface rounded and sunken towards peristome. Apical disc with five gonopores; genital plate 2 is enlarged and occupies the centre of the disc; the other genital plates are reduced in size and the posterior ones are separated from one another by ocular plates. Ambulacral plating simple from apex to subambital region; trigeminate adorally; pore-pairs uniserial and undifferentiated. Periproct large, extending from close to the peristome to the ambitus, so that it is visible in posterior view. Tuberculation of interambulacral plates consists of a row of small primary tubercles, becoming offset slightly near the adradius, separated by a single dense row of miliary tubercles.

OCCURRENCE. Maastrichtian, horizons 2, 5 and 7/8, Santander. Maastrichtian, horizon 6, Olazagutia Pass, Navarra. Lower Maastrichtian of the Homes Morts Member at Sapeira and Santa Engràcia, Tremp Basin (Gallemí, 1992). The type comes from the Maastrichtian of Roquefort (Haute-Garonne), France.

MATERIAL STUDIED. BMNH EE6129–31, MGB 37499.

REMARKS. Easily distinguished from the other holectypoid found here, *Camerogalerus cantabricus* sp. nov., by the large size of its periproct and by its much lower and wider ambital plates. It also has much better aligned miliary granulation. Krumbeck (1906) erected the species *Discoidea Nactigali* on the basis of specimens from the Maastrichtian of Libya. From the rather sketchy illustrations and

description these cannot be distinguished from Lambert's species. Unfortunately, Krumbeck's types were destroyed during the Second World War and the original descriptions and figures are inadequate to be fully confident about its true identity.

Genus **CAMEROGALERUS** Quenstedt, 1873

DIAGNOSIS. Holectypids with internal buttresses along adradial margins of interambulacral plates on oral surface. Genital plates all equal in size with madrepores generally distributed across all five plates.

Camerogalerus cantabricus Smith & Gallemí, sp. nov. Pl. 2, figs 9–11; Fig. 8a–c

TYPES. Holotype EE6132; paratype MGB37577.

DIAGNOSIS. Small, hemispherical species up to 7 mm in diameter. Circular in outline, subconical in profile (height 64% of diameter) with ambitus at about one-third test height; lower surface convex, hardly sunken towards the peristome. Apical disc with five gonopores. Ambulacra straight, with uniserial pore-pairs; plating simple above ambitus, but in triads from ambitus adorally with one and then two demiplates in each triad. Interambulacra composed of relatively tall, narrow plates. Tuberculation comprises scattered primary tubercles set amongst irregularly arranged miliary granules. Peristome very small, 1.5 mm in diameter (22 % test diameter), with feeble buccal notches. Periproct also very small and situated close to the peristome; separated by just 2 plates from the peristome; distance from periproct to ambitus is much greater than distance separating the periproct and peristome. Internal buttressing narrow and blade-like and extending to the ambitus (seen on MGB 37577 where the oral surface is damaged).

OCCURRENCE. Maastrichtian, horizon 2 (paratype) and 4 (holotype), Santander.

REMARKS. Distinguished from *Coenholectypus nactigali* by the much smaller size of its periproct, its more inflated profile and by its very different tuberculation.

Order **ECHINONEOIDA** Clark, 1925 Family **CONULIDAE** Lambert, 1911

DIAGNOSIS. Irregular echinoids with a compact apical disc with four genital plates. Ambulacra with pyrinoid plating; pore-pairs undifferentiated. Peristome small, circular to elliptical, lacking buccal notches. Tubercles small, dense, uniform and sunken.

Genus **CONULUS** Leske, 1778

DIAGNOSIS. Conulids with pyrinoid ambulacral plating throughout. Periproct marginal to inframarginal. Pore-pairs forming widened bands adorally.

Conulus gigas (Cotteau, 1856) Pl. 3, figs 1, 2

- 1856 *Echinoconus gigas* Cotteau, in Leymerie & Cotteau: 330.
1860 *Echinoconus gigas* Cotteau; Cotteau, in d'Orbigny, 1853–60: 511, pl. 994, fig. 6; pl. 995, figs 1–5.
1907 *Conulus gigas* (Cotteau); Lambert: 707.
1992 *Conulus gigas* (Cotteau); Gallemí: 146, figs 45–47.
1995 *Conulus gigas* (Cotteau); Gallemí *et al.*: 269, tab. 1.

DIAGNOSIS. Test up to 70 mm in length; width approximately 90% of length; height approximately 67% of length. Domed in profile

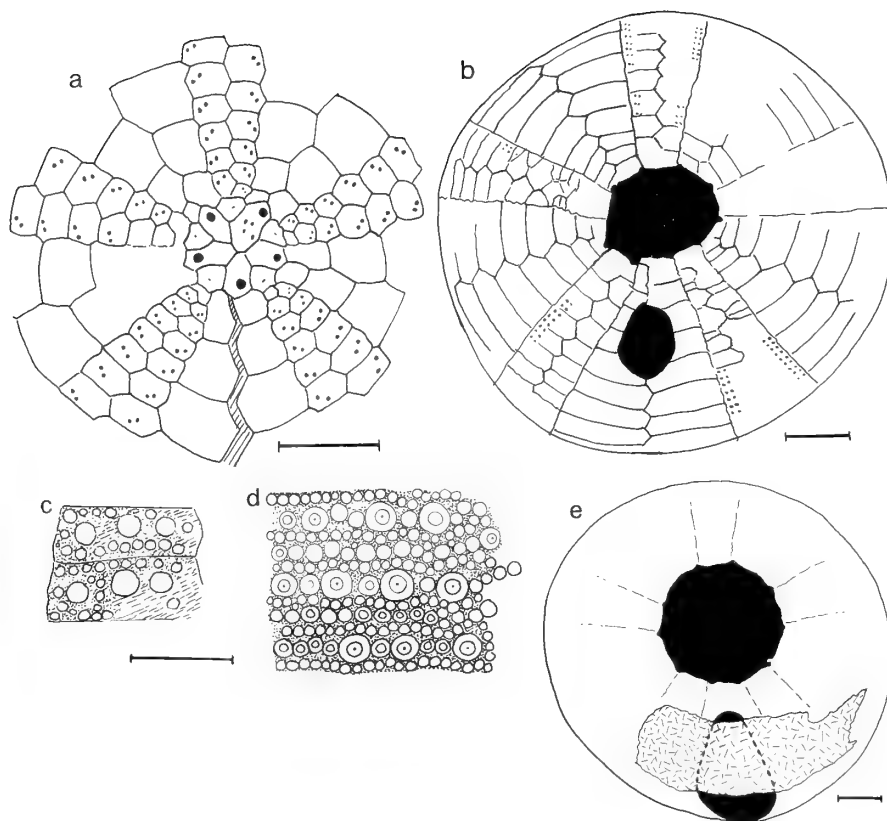


Fig. 8 Camera lucida drawing of plating: **a–c**, *Camerogalerus cantabricus* sp. nov. BMNH EE6132 (holotype); Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); **a**, apical disc; **b**, oral surface; **c**, supraambital interambulacral plates. **d, e**, *Coenholectypus nachtigali* (Krumbeck, 1906), Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); **d**, BMNH EE6129; supraambital interambulacral plates; **e**, BMNH EE6131, oral view. Scale bars = 1 mm.

with ambitus set low down. Periproct longitudinal, just subambital and clearly visible in posterior view. Oral surface pulvinate with small subcircular central peristome. Ambulacral pore-pairs forming broad bands over much of the oral surface.

MATERIAL STUDIED. BMNH EE4351–5, EE6131–33, MGB 37471, 37511, 37542, 37557.

OCCURRENCE. Maastrichtian, horizons 4, 5, 6 and 7/8, Santander. Lower Maastrichtian of the Homes Morts Member at Sapeira, Santa Engràcia and Salàs de Pallars, Tremp Basin (Gallemí, 1992). Maastrichtian, top of bed 1, Olazagutia Pass, Navarra. Maastrichtian of Mas de Santa Maria, near Ibi, Alicante province (Gallemí *et al.*,

1995). The type comes from the Maastrichtian of Saint Proupiary, near Auzas, Haute-Garonne, France and it has also been recorded from numerous other localities in Haute-Garonne, including Ausseing Massif, Picou near Roquefort, Mont Saunès, Beauchalot, Saint-Martory and Salies (Lambert, 1907).

REMARKS. Differs from *C. magnificus* (d'Orbigny) in having a longitudinal rather than transverse periproct, and from *C. douvillei* (Cotteau & Gauthier) in having a small, almost circular peristome as opposed to the distinctly oblique and large peristome of that species. This species becomes most common between levels 6 and 8 in the Maastrichtian of Santander.

PLATE 3

Figs 1, 2 *Conulus gigas* (Cotteau, 1856), BMNH EE4354, Maastrichtian of Santander, Cantabria. Oral and lateral views, $\times 1$.

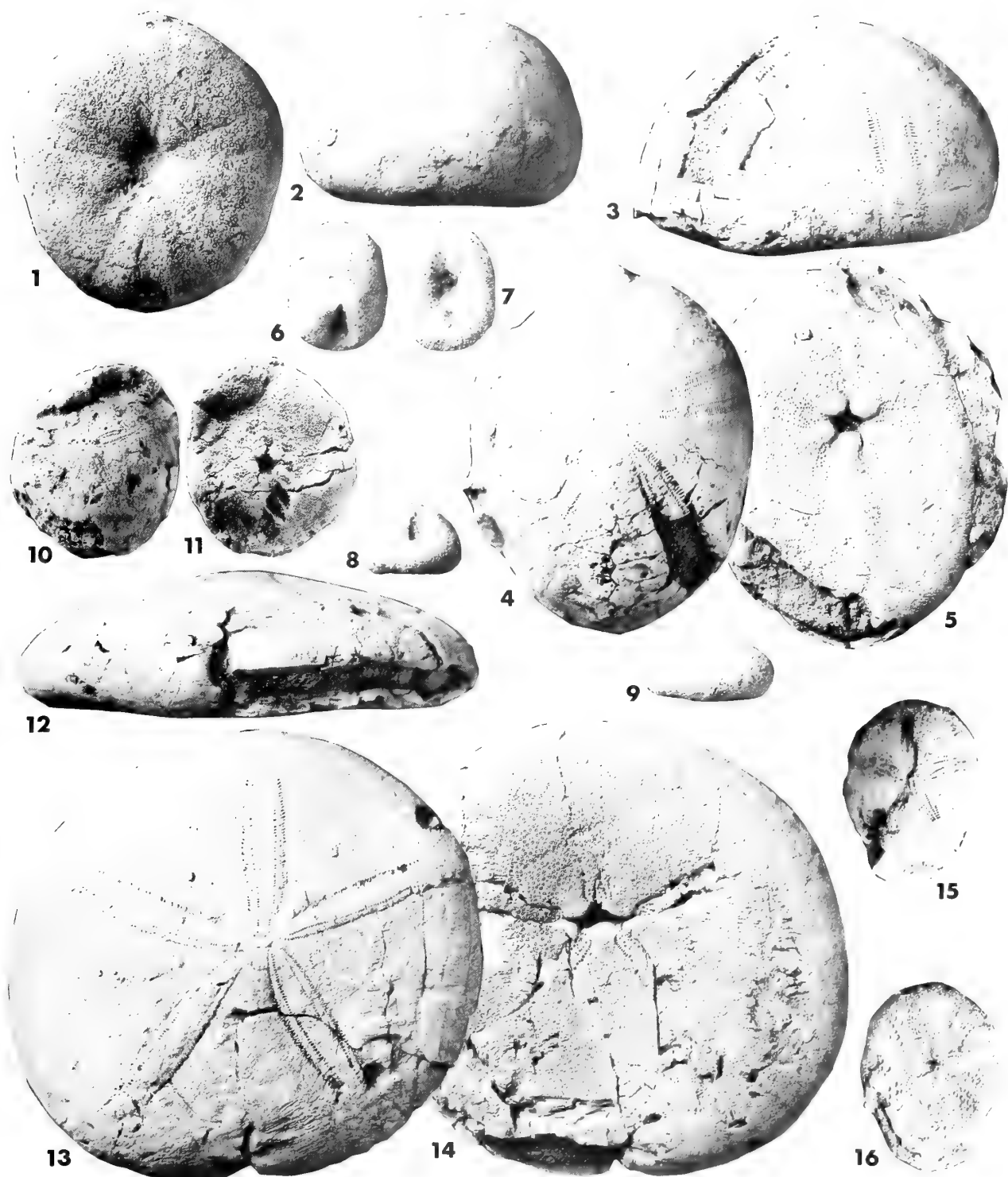
Figs 3–5 *Clypeolampas ovatus* (Lamarck, 1816), BMNH EE6144, Maastrichtian of Santander, Cantabria. Lateral, apical and oral views, $\times 1$.

Figs 6–9 *Nucleopygus coravium* (Agassiz, in Agassiz & Desor, 1847), BMNH EE6148, Maastrichtian of Santander, Cantabria. Apical, oral, posterior and lateral views, $\times 3$.

Figs 10, 11 *Zuffardia* sp., BMNH EE6153, Maastrichtian of Santander, Cantabria. Apical and oral views, $\times 1.5$.

Figs 12–14 *Gitolampas subrotundus* (Cotteau, 1856), BMNH EE6173, Thanetian of Santander, Cantabria. Posterior apical and oral views, $\times 1$.

Figs 15, 16 *Rhyncholampas macari* (Smiser, 1935), MGB37512, Maastrichtian of Santander, Cantabria. Apical and oral views, $\times 1.5$.



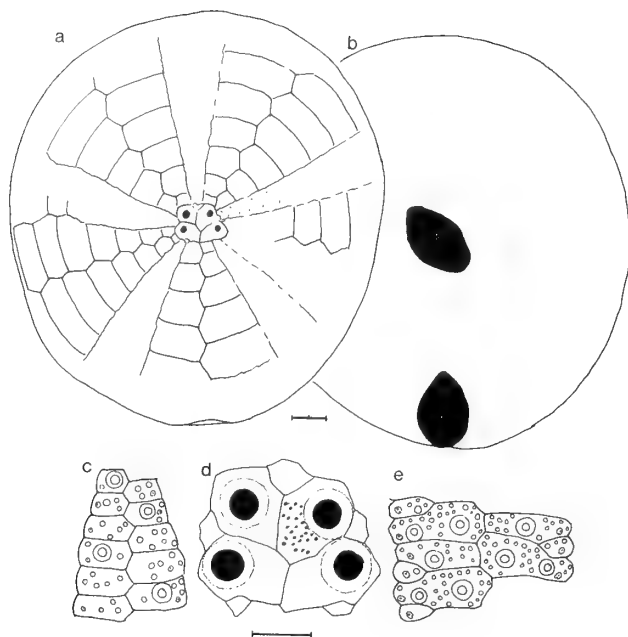


Fig. 9 Camera lucida drawings of plating in *Adelopneustes ernsti* sp. nov. from Casas de Oraien (Navarra); BMNH EE6134, a, apical surface; b, oral surface; c, adapical ambulacrum; d, apical disc; e, subambital ambulacrum. Scale bars: a, b = 2 mm; c-e = 1 mm.

Genus *ADELOPNEUSTES* Gauthier, 1889

DIAGNOSIS. Conulids with pyrinoïd ambulacral plating orally and simple plating aborally. Peristome subcircular to weakly elliptical.

Adelopneustes ernsti Smith & Gallemí, sp. nov.

Pl. 2, figs 5-8; Fig. 9

DIAGNOSIS. Test ovate in outline, slightly pointed to rear; 26 mm in length, slightly narrower than long; low-domal in profile, with test height 14.5 mm. Apical disc tetrabasal with large gonopores surrounded by rims (female character only?); subcentral on genital plates. Ambulacral pores very small and rudimentary, almost impossible to see even under magnification; double adapically. Ambulacral plating apparently simple aborally; plating adorally not visible. Peristome oblique (crushed in the only specimen known), elongate towards anterior left. Lower surface strongly rounded. Periproct elongate and pointed both adorally and adapically, visible from beneath and posteriorly; as large as mouth.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Larumbe, Navarra province, Spain.

TYPES. Holotype, BMNH EE6134.

REMARKS. Differs from *N. boehmi* (Neitsch) in having a more depressed profile and larger gonopores surrounded by a raised platform. Differs from *N. montainvillensis* (Sorignet) in having an oblique rather than circular peristome. Differs from both these species and from all others assigned to this genus in having rudimentary aboral pores.

Order CASSIDULOIDA Claus, 1880

DIAGNOSIS. Peristome small, lacking buccal notches; interambulacra undifferentiated. Ambulacral pores differentiated into aboral petals and oral phyllodes, though occasionally rudimentary throughout.

Family PLACHIOCHASMIDAE Smith & Jeffery, in press

Genus *ECHINO GALERUS* König, 1825

DIAGNOSIS. Peristome small, anterior of centre. Periproct slightly wider than long, inframarginal. Petals and phyllodes rudimentary.

Echinogalerus muelleri (Schlüter, 1902)

Pl. 2, figs 17-20; Fig. 10b, d

1902 *Caratomus Muelleri* Schlüter: 316, pl. 11, figs 14-17.

1927 *Echinogalerus belgicus* Lambert: 38.

1987 *Echinocyamus muelleri* Schlüter; Van der Ham *et al.*: 28, pl. 9, fig. 3.

1992 *Echinogalerus muelleri* Schlüter; Van der Ham & Van Birgelen: 149, pl. 3, fig. 7.

1992 *Echinogalerus belgicus* Gallemí: 170, photo 6.

DIAGNOSIS. Test up to 15 mm in length; width about 85-90% of length; height about 60% of test length. Ovate in outline with rounded anterior and widest point slightly posterior to midlength. Depressed in profile with rounded margins; lower surface strongly pulvinate and slightly sunken towards peristome; upper surface depressed. Ambulacra composed entirely of simple plating; ambulacral pores double throughout, almost subpetaloid adapically in largest individuals; uniserial adorally. Pore-pairs oblique and strictly uniserial towards the peristome; widely separated. Peristome slightly anterior of centre; relatively large (13% of test length); oblique along 3-V axis. Periproct subambital, clearly visible in oral view; transverse, wider than the peristome, subtrigonal and pointed adorally; separated from the peristome by about 4 interambulacral plates. Tuberculation of scattered sunken tubercles.

OCCURRENCE. Maastrichtian, horizons 3 to 6, Santander, Cantabria; Maastrichtian, horizon 6, Olazagutia Pass, Navarra province. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars and Sapeira, Tremp Basin (Gallemí 1992). The type comes from the Upper Maastrichtian of Vetschau, near Aken, Germany.

MATERIAL STUDIED. BMNH EE4412(a-d), EE4413(a-f), EE6137-38, EE6163; MGB 37451-57, 37490-98, 37500-02, 37526, 37528, 37532, 37537, 37546.

REMARKS. Similar in shape to *E. belgicus*, but with double pores in its ambulacra. Differs from *E. vetschauensis* in having a larger peristome, more pulvinate lower surface and strictly uniserial pore-pairs adorally. Populations from Tremp and from Olazagutia Pass contain both large and small individuals, and are assigned to this species without doubt. However, only small individuals have so far been found at horizons 3 and 5 at Santander. Because these are indistinguishable from small individuals that we have from Olazagutia, we have included them in this species.

Echinogalerus? vetschauensis (Schlüter, 1902)

Pl. 2, figs 13-16; Fig. 10a, c

1902 *Caratomus vetschauensis* Schlüter: 318, pl. 11, figs 10-13.

1987 *Echinogalerus vetschauensis* Schlüter; Van der Ham *et al.*: 28, pl. 9, fig. 5.

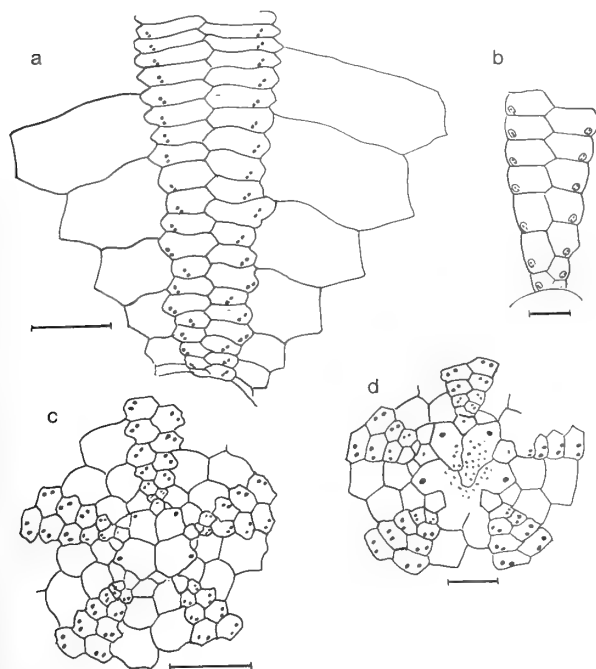


Fig. 10 Camera lucida drawings of plating in *Echinogalerus* species. **a, c**, *E. vetchauensis* (Schlüter, 1902) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **a**, BMNH EE6164, adoral ambulacrum, peristome opening at base; **c**, BMNH EE 6165, apical disc; **b, d**, *E. muelleri* (Schlüter, 1902), BMNH EE4412a from Olazaguti pass, Navarra; **b**, adoral ambulacrum I, peristome margin at base; **d**, apical disc. Scale bars = 1 mm.

DIAGNOSIS. Test up to 12 mm, width *ca.* 95% of length, height *ca.* 60% of length. Outline ovate with widest point at midlength; depressed in profile, with relatively flat base. Apical disc tetrabasal with posterior genital plates abutting. Ambulacra narrow; pores double aborally, but small, oblique and widely spaced; pores uniserial except adorally where they are arranged into oblique arcs of three. All ambulacral plating simple. Peristome small (6–7% of test length along the anterior-posterior axis); slightly oblique. Periproct subambital, transverse and trigonal; only slightly larger than the peristome in length, but considerably wider. Tuberculation relatively dense over the oral surface.

OCCURRENCE. Maastrichtian, horizons 2 and 4, Santander. The type comes from the Upper Maastrichtian of Vetschau, near Aken, Germany. It is also known from the Kurade limestone facies, Upper Maastrichtian of the Maastricht region.

MATERIAL STUDIED. BMNH EE6134–36, EE6164–66, MGB 37522.

REMARKS. Distinguished from *E. muelleri* by its flatter lower surface, its much smaller peristome and by having pore-pairs offset into triads towards the peristome. These features also separate *E. vetchauensis* from *E. belgicus*, but in addition, *E. belgicus* (at least as interpreted in Van der Ham *et al.*, 1987) has rudimentary aboral pores aborally that appear to be single.

This species bears a strong resemblance to *Galerites sulcatoradiatus* (Goldfuss), a species that grows to much greater size. Both have offset pore-pairs adorally and both have a similar

small peristome and periproct. With further study, and better and more diverse material, *E. vetchauensis* may turn out to be simply small individuals of *G. sulcatoradiatus*.

Family ECHINOLAMPADIDAE Gray, 1851

Genus GITOLAMPAS Gauthier, 1889

DIAGNOSIS. Ovate to subpentagonal in outline; oral surface planar; margins rounded; upper surface planar to low subconical. Apical system tetrabasal or monobasal, anterior of centre, with four gonopores. Periproct longitudinal; opening on posterior surface within shallow sulcus. Petals subparallel, open distally; pore columns subequal. Peristome anterior, pentagonal, transverse, with vertical-walled vestibule. Phyllodes moderately well developed, with an outer and inner series of pores, the outer series being slightly bowed. No bourrelets. Basicoronal interambulacral plates wider than long. Buccal pores present. A narrow zone free of primary tubercles runs along the interradiar suture between the peristome and posterior border.

Gitolampas subrotundus (Cotteau, 1856)

Pl. 3, figs 12–14

- 1856 *Pygorhynchus subrotundus* Cotteau, in Leymerie & Cotteau: 334.
- 1857 *Echinanthus subrotundus* Desor, in Desor 1855–58: 293.
- 1888 *Echinanthus subrotundus* Desor; Cotteau, in Cotteau 1885a–89a: 586, pls 173, 174, pl. 175, figs 1–3.
- ?1908 *Echinanthus arizensis* Cotteau; Lambert: 366.
- 1908 *Echinanthus Heberti* Cotteau; Lambert: 367.
- ?1908 *Echinanthus Cotteaui* Hébert; Lambert: 368.
- 1908 *Echinanthus Gourdoni* Cotteau; Lambert: 368.
- 1975 *Echinanthus arizensis* Lambert; Plaziat *et al.*: 631, pl. 2, figs 1, 3.

DIAGNOSIS. Test up to 87 mm in length; width 85–95% of length, height *ca.* 30–36%. Outline subcircular to weakly ovate and somewhat pointed at the posterior; lower surface relatively flat or slightly sunken towards the peristome, with rounded margins. Upper surface low domal. Apical system obscured in our specimens, but probably monobasal; lying 40% test length from the anterior border. Petals well developed, extending most of the distance to the ambitus in plan view; equally wide with interpore zone twice the width of the pore zone; open distally. Anterior petal extending 75–80% the distance to the ambitus in plan view, posterior petals extending 70–80% the distance. Peristome 40% test length from the anterior; strongly transverse and pentagonal. Phyllodes moderately well developed consisting of an outer series of *ca.* nine pores and inner series of two or three pores. Buccal pores present at outer margin of vestibular entrance to peristome.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, horizon 10, Santander. Also known from Lower Thanetian to Lower Ypresian localities in the French and Spanish Pyrenees and the Villarcayo basin (Burgos province, northern Spain). The type (Leymerie collection, Toulouse) comes from the 'Montian' of Fabas (Ariège, France), and it is also known from several other localities in Ariège (Sabarat, le Mas-d'Azil, Campagne, Montardit, Camarade and Saint-Jean-de-Verges) and Haute-Garonne (Martres, Saint-Marcel, Aurignac, Montbrun, Marsoulas).

MATERIAL STUDIED. BMNH EE6173, MGB 37573.

REMARKS. This species is easily distinguished from others

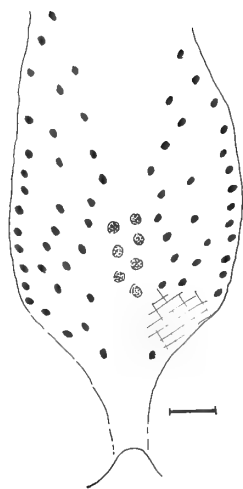


Fig. 11 Camera lucida drawing of plating in *Clypeolampas ovatus* (Lamarck, 1816) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6144, phyllode of ambulacrum II, peristome margin at base. Scale bar = 1 mm.

reported here, by its large size, strongly transverse peristome and posterior longitudinal periproct. There are many species of *Gitolampas* recognized from the Maastrichtian and Palaeocene (Smith & Jeffery, in press). It is distinguished from the closely similar *G. ataxensis* (Cotteau) by the form of its petals, which are more bowed and proportionally longer than in *G. ataxensis*.

Family CLYPEOLAMPADIDAE Kier, 1962

Genus CLYPEOLAMPAS Pomel, 1869

DIAGNOSIS. Test with flat base and highly vaulted upper surface. Petals long, extending almost to the ambitus; slightly expanding and widely open distally. Periproct submarginal at rear of oral surface; transverse. Narrow granular sternal zone present behind periproct. Phyllodes widely expanded, with many pores scattered between the inner and outer series. Interambulacra swollen towards peristome with 'bourrelets' composed of many small plates rather than just a single large basicoronal plate.

Clypeolampas ovatus (Lamarck, 1816)

Pl. 3, figs 3–5; Fig. 11

- 1816 *Galerites ovatus* Lamarck, 1816: 22.
 1829 *Clypeaster leskei* Goldfuss, 1829: 132, pl. 42, fig. 1.
 1920 *Clypeolampas leskei* Goldfuss; Lambert: 21.
 1996 *Clypeolampas* cf. *ovatus* (Lamarck); Wilmsen *et al.*: fig. 7.

DIAGNOSIS. As for genus.

OCCURRENCE. Maastrichtian, horizons 1, 2 and 4, Santander; Maastrichtian, Somo Beach, near Santander, Cantabria province. Upper Campanian of Barranc d'en Jaume, Quatretonda and Nicolasa quarry, Tavernes, Valencia province, Spain (Nicklès 1892). This species is widely reported from the Maastrichtian of the Anglo-Paris Basin, Charente-Maritime and Dordogne, France.

MATERIAL STUDIED. BMNH EE6144–47.

REMARKS. This species is moderately common in the shallowest limestones at the base of the transgressive Maastrichtian sequence at Santander. Several species have been distinguished by Lambert (1920) on material from the Santander region. The differences between his species *C. mengaudi*, *C. douvillei* and *C. ovatus* are based on the disposition of pores in the phyllodes. Although there are certainly slight differences, it is not at all clear how much individual variation exists in this character within single populations, and the three taxa may well turn out to be conspecific.

Unnamed Family

Genus NUCLEOPYGUS Agassiz, 1840

DIAGNOSIS. Subquadrate in outline and depressed in profile, with supramarginal periproct opening into subanal sulcus. Apical disc tetrabasal. Ambulacra subpetaloid at most. Peristome lacking bourrelets; perioral tuberculation confined to peristomial well. Phyllodes generally rather undeveloped with every third pore-pair insert.

Nucleopygus coravium (Agassiz, in Agassiz & Desor, 1847)

Pl. 3, figs 6–9; Pl. 4, figs 7–9

- 1847 *Nucleopygus cor avium* Agassiz; Agassiz & Desor: 152.
 1898b *Nucleopygus coravium* Lambert: 168, pl. 5, figs 1–4, 8–14.
 1935 *Nucleopygus coravium* Smiser: 52, pl. 5, fig. 1.
 1987 *Nucleopygus coravium* Van der Ham *et al.*: 29, pl. 11, fig. 2.

DIAGNOSIS. Small species, rarely reaching more than 10 mm in length; width ca. 75% of length; depressed with height ca. 50% of length. Ovoid in outline with a rounded anterior and slightly truncated posterior; widest point posterior of centre. In posterior profile the test is strongly concavo-convex. Apical system anterior, about one-third of test length from the anterior; tetrabasal with posterior genital plates not separated by the madreporite; genital plate 3 smaller than the remainder. Petals small and rudimentary, particularly the anterior petal; lateral and posterior petals equally developed, the posterior pair ending well before reaching the level of the periproctal opening. Pore-pairs weakly conjugate with equal-sized pores. Peristome large, oval to subpentagonal, slightly anterior of centre, depressed with inwardly sloping margins. Phyllodes more or

PLATE 4

Figs 1–6 *Nucleopygus scrobiculatus* (Goldfuss, 1829), Maastrichtian of Santander, Cantabria. **1**, BMNH EE6157; apical view, $\times 2$. **2–4**, BMNH 6156; oral, lateral and posterior views, $\times 2$. **5, 6**, BMNH EE6154; oral and posterior views, $\times 2$.

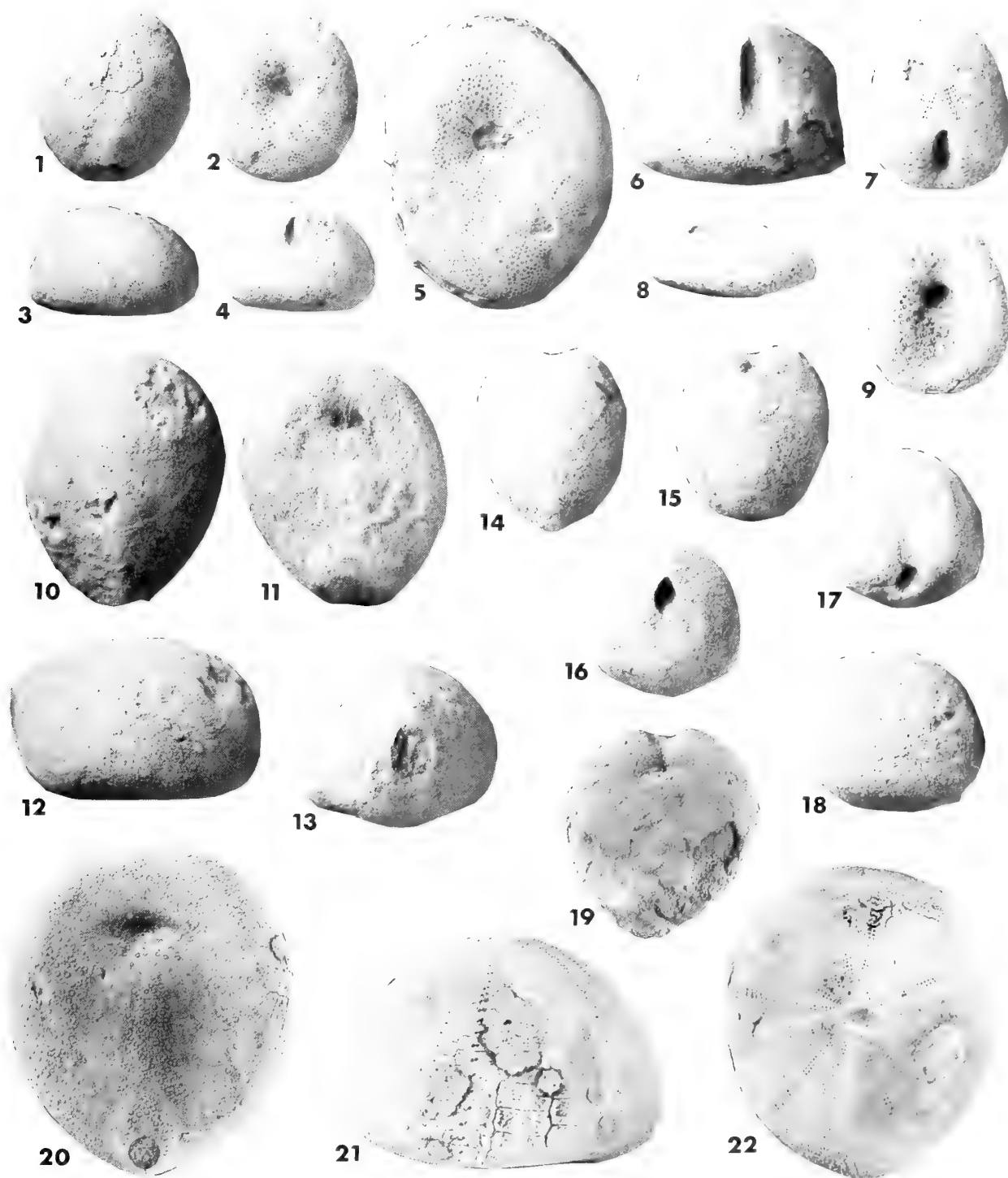
Figs 7–9 *Nucleopygus coravium* (Agassiz, in Agassiz & Desor, 1847), BMNH EE4403, Maastrichtian of Olazagutia Pass, Navarra. Apical, lateral and oral views, $\times 3$.

Figs 10–13 *Offaster leymeriei* Cotteau, 1887, BMNH EE6170, Maastrichtian of Santander, Cantabria. Apical, oral, lateral and posterior views, $\times 1.5$.

Figs 14–18 *Galeaster bertrandi* Seunes, 1889, BMNH EE6188, Maastrichtian of Santander, Cantabria. Apical, oral, posterior, anterior and lateral views, $\times 2$.

Fig. 19 *Cardiaster* sp. BMNH EE6174, Thanetian of Casas de Oraien, Navarra. Oral view, $\times 1$.

Figs 20–22 *Echinocorys scutata* forma *cotteaui* Lambert, 1903, BMNH EE6189, Thanetian of Casas de Oraien, Navarra. Oral, lateral and apical views, $\times 1$.



less uniserial to peristome, with no pore crowding whatsoever. Small buccal pores are present at the peristomial margin. Periproct oval, longitudinal, in distinct anal sulcus opening closer to the posterior margin than the apical system.

OCCURRENCE. Maastrichtian, horizon 2 (top) and 4, Santander; Maastrichtian, horizon 6, Olazagutia Pass, Navarra province. This species also occurs in the upper Lower to lower Upper Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987), the Maastrichtian 'Craie phosphatée' at Ciply, Belgium (Lambert, 1898b) and the Maastrichtian at Fresville, Manche, France (Lambert collection).

MATERIAL STUDIED. BMNH EE4403, EE6148–49, MGB 37519.

REMARKS. This is a small species of juvenile appearance (simple short petals, simple phyllodes, absence of bourrelets). There are several names available for such forms, but they lack distinctive characters and are virtually impossible to separate. Consequently, we group all together here under the name *N. coravium* Defrance.

This species is readily distinguished from the co-occurring *N. scrobiculatus* by its shape, which is much less tumid and with a deeply sunken oral surface, and by its phyllodes, which are completely undifferentiated. It differs from *N. geayi* in having a more posterior periproctal opening.

Nucleopygus scrobiculatus (Goldfuss, 1829)

Pl. 4, figs 1–6; Fig. 12

1829 *Nucleolites scrobiculatus* Goldfuss: 138, pl. 43, fig. 3.

1935 *Lychnidius scrobiculatus* (Goldfuss); Smiser: 49, pl. 4, fig. 10.

1957 *Nucleopygus scrobiculatus* (Goldfuss); Engel & Meijer: 88, pl. 1.

1987 *Nucleopygus scrobiculatus* (Goldfuss); Van der Ham *et al.*: 30, pl. 11, fig. 3.

DIAGNOSIS. Test up to 26 mm in length, ovate; width 85–90% of length, widest centrally; height 60–65% of length, tallest behind apical disc. Apical disc a little anterior of centre (40% of length); tetrabasal with four gonopores. Petals subequal with almost parallel columns. Periproct supraambital, but positioned far to the posterior on the steeply sloping posterior face; longitudinal with anal sulcus only pronounced in juveniles. Oral surface strongly pulvinate with peristome deeply invaginated. Peristome transverse and rounded pentagonal. Phyllodes hardly expanded adorally, with a single series of pores, becoming offset close to the peristome in specimens up to 15 mm length; with one pore in each of the first two groups of three insert in larger individuals. Peristome with deep tuberculate vestibule leading into peristome; buccal pores near top of this vestibule. No bourrelets. Narrow granular tubercle-free zone present posterior to the peristome.

OCCURRENCE. Maastrichtian, horizon 4, Santander; Maastrichtian, horizon 6, Olazagutia Pass, Navarra.

MATERIAL STUDIED. BMNH EE6154–61, MGB 37458, 37517

REMARKS. We have slight reservations about uniting our material with *N. scrobiculatus*. The holotype of *N. scrobiculatus* was established for a 7 mm individual. Later additional specimens were described by Engel & Meijer (1957) and Van der Ham *et al.* (1987) up to 21 mm in length. Small individuals from Santander and Olazagutia correspond very closely with the Maastricht population. However, larger specimens become progressively less similar, showing a less pulvinate lower surface, more rostrate posterior and phyllodes with more offset pores. When we consider the full range of

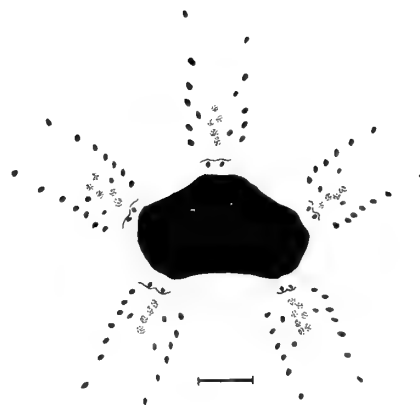


Fig. 12 Camera lucida drawing of plating in *Nucleopygus scrobiculatus* (Goldfuss, 1829) from the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6154, phyllodes and peristome margin. Scale bar = 1 mm.

sizes present at Santander, there is no clear-cut separation between the smaller and larger individuals. We therefore conclude that the small differences are growth-related and that all our material belongs to the same species.

This species differs from *N. coravium* in having the periproct positioned on the steeply sloping part of the test, much closer to the posterior margin, in being much more pulvinate with a more rounded ambitus, and in lacking a strong saggital depression on its oral surface.

Family CASSIDULIDAE Agassiz & Desor, 1847

Genus *OOLOPYGUS* d'Orbigny, 1856

DIAGNOSIS. Elongate cassiduloids with flat base and subcentral, pentagonal peristome surrounded by weak bourrelets, and widened phyllodes comprising inner and outer series. Apical disc with three gonopores, no gonopore present in anterior left portion of disc. Petals rudimentary to poorly developed. Broad pitted tubercle-free zone present both anterior and posterior to the peristome.

Oolopygus sp.

Fig. 13a

OCCURRENCE. Maastrichtian, horizon 5, Santander.

MATERIAL STUDIED. BMNH EE6169.

REMARKS. Our solitary specimen is a small individual just under 10 mm in length. It is too small to be identified with certainty to species level, but has sufficient characters to be confident about its generic identity. Specifically, it possesses only three large gonopores, and the oral surface is flat with a small subcentral mouth. Bourrelets are small but distinct, and a granular naked zone is developed on the oral surface. It may be a juvenile individual of *O. pyriformis* (Lamarck), the Maastrichtian species that is found in the Maastricht area. However, at this size it also bears close resemblance to *Oolopygus rostriformis* (Kadilnikova & Moskvina) from the Palaeocene of Mangyshlak, Kazakhstan.

Genus *RHYNCHOPYGUS* d'Orbigny, 1856

DIAGNOSIS. Small cassiduloids with a flat base and low domal profile. Peristome small, subcentral, surrounded by weak bourrelets

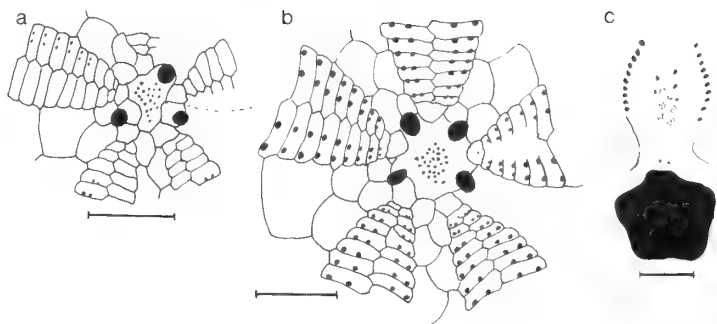


Fig. 13 Camera lucida drawings of plating in *Oolopygus* sp. and *Zuffardia* sp. from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **a**, *Oolopygus* sp., BMNH EE6169, apical disc; **b**, *Zuffardia* sp., BMNH EE6153; **b**, apical disc; **c**, phyllode and peristome margin. Scale bars = 1 mm.

and with V-shaped phyllodes comprising a single series of pores. Periproct supra-ambital, on the underside of a large lobate projection; opening appears wide and slit-like in posterior profile. Oral tuberculation arranged with a strong bilateral symmetry.

Rhynchopygus sp.

OCCURRENCE. Maastrichtian, horizon 4, Santander

MATERIAL STUDIED. BMNH EE6162.

REMARKS. Our record is based on a single specimen, representing the posterior portion of a test. This shows the highly characteristic lobe-like projection above the wide and slit-like periproctal opening. There are two species of *Rhynchopygus*, *R. marmini* (Agassiz) and *R. donetzensis* (Faas), differing primarily in the development of their petals. As our specimen does not show the petals, it cannot be assigned to species level.

Genus *RHYNCHOLAMPAS* Agassiz, 1869

DIAGNOSIS. Small cassiduloids with a flat base and ovate outline. Peristome small, subcentral, weakly transverse to as wide as long; rim of peristome hardly swollen; deep well leading into peristomial opening. Periproct supra-ambital; transverse, hardly sunken.

Rhyncholampas macari (Smiser, 1935) Pl. 3, figs 15, 16

1935 *Rhynchopygus macari* Smiser: 63, pl. 6, fig. 6.

1987 *Procassidulus macari* (Smiser); Van der Ham *et al.*: 30, pl. 11, fig. 6.

DIAGNOSIS. Test up to 33 mm in length; elongate with flat base and depressed upper surface. Width 75–80% of length, widest posterior of mid-length; height no more than 35% of length. Apical disc a little anterior of centre, with four gonopores; probably tetrabasal, but plating not seen. Petals well-developed, bowed and converging distally; posterior petals shorter than lateral and anterior petals. Peristome slightly anterior of centre; small and pentagonal; almost as wide as long; surrounded by small but distinctly swollen bourrelets. Phyllodes composed of a V-shaped outer series of pores plus one or two inner pores near the apex of the V. Broad pitted sagittal zone free of tubercles both anterior and posterior to the peristome. Periproct supramarginal; transverse, with slight aboral canopy.

OCCURRENCE. Maastrichtian, bed 4, Santander. This species also occurs in the Lichtenberg Horizon, and Nekum and Meerssen Mem-

bers, Maastricht Formation, *B. junior* and *B. kazimiroviensis* Zones, Upper Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987).

MATERIAL STUDIED. BMNH EE6150–52, MGB 37512

REMARKS. Although our material is unfortunately rather crushed, all relevant plating details are seen, allowing us to be confident in our determination. No other cassiduloid described herein has a transverse periproct situated supra-ambitally.

Family FAUJASIIDAE Lambert, 1905

Genus *ZUFFARDIA* Checchia-Rispoli, 1917

DIAGNOSIS. Globose cassiduloids with monobasal apical disc and relatively short petals. Peristome small, subcentral, pentagonal, surrounded by distinct phyllodes and bourrelets. Periproct posterior, hardly invaginated. All pores below petals single.

Zuffardia sp.

Pl. 3, figs 10, 11; Fig. 13b, c

DIAGNOSIS. Test up to 25 mm in length; almost subcircular in outline, inflated in profile with flat to weakly convex base and subcentral peristome. Apical disc compact, with four gonopores. Petals relatively short and weakly bowed; extending about half the distance to the ambitus. Peristome small, pentagonal, surrounded by small bourrelets. There is a deep well leading into the peristomial opening. A broad naked pitted zone is developed both anterior and posterior to the peristome on the oral surface. Periproct posterior, subcircular, hardly invaginated. Phyllodes well developed with bowed outer series of ten pores separated from three inner series pores. All pores single below the petals.

OCCURRENCE. Maastrichtian, horizon 4, Santander.

MATERIAL STUDIED. BMNH EE6153, MGB 37521, 37525, 37527.

REMARKS. Resembles *Catopygus fenestratus* Agassiz & Desor in general appearance, but distinguished from that species by having entirely single pores below the petals, and in having a well-developed anterior and posterior naked zone that is pitted. This latter feature distinguishes it from the type species *Z. morgani* (Cotteau & Gauthier), which has an unpitted naked zone adorally. Very similar material was described from the Late Maastrichtian, *B. kazimiroviensis* Zone of Mangyshlak by Jeffery (1997). Our speci-

mens are, however, too poorly preserved to form the basis for formally erecting a new species name.

Order **HOLASTEROIDA** Durham & Melville, 1957

DIAGNOSIS. Irregular echinoids with meridosternous or orthosternous plastron, paired ambulacra flush on test; apical disc elongate with one or both ocular plates inserted between anterior and posterior pairs of genital plates.

Family **HOLASTERIDAE** Pictet, 1857

Genus **OFFASTER** L. Agassiz, 1836

DIAGNOSIS. Small holasteroids with flat to slightly convex base and vaulted upper surface. Apical disc with four gonopores. Frontal groove absent aborally, slightly depressed at ambitus and subambitally, at least in small individuals. Peristome oval to D-shaped; facing downwards, with little or no labral projection. Plastron meridosternous with first two to three plates uniserially arranged. Periproct on posterior face. Marginal fasciole present, at least in juvenile stages; possibly absent in larger individuals.

Offaster leymeriei Cotteau, 1887

Pl. 4, figs 10–13; Figs 14, 15

1887b *Offaster Leymeriei* Cotteau: 661, pl. 19, figs 14, 15, pl. 20, figs 1–3.

?1927 *Offaster dallonii* Lambert: 43, pl. 3, figs 12–15.

1992 *Offaster dallonii* Gallemí: 257, photo 14.

1996 *Offaster dallonii* Wilmsen et al.: fig. 7.

DIAGNOSIS. Test up to 30 mm in length; width ca. 80–85% length; height ca. 65% of length. Ovate in outline; specimens larger than about 15 mm with convex anterior, smaller individuals with slight anterior sulcus developed from ambitus adorally. Peristome moderately large, oval, 15% test length from the anterior. Periproct large, occupying the upper part of the posterior face, which slopes very slightly inwards so that the periproct is just visible from below but not from above. Plastron plating meridosternous. Tuberculation relatively fine, with no primaries differentiated aborally. Small individuals show a clear marginal fasciole around the posterior margin of the test; this fasciole may be lost in large individuals.

OCCURRENCE. Maastrichtian, horizons 3 and 5, Santander. Maastrichtian, horizons 5 and 6, Olazagutia Pass, Navarra. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars, Tremp Basin (Gallemí, 1992). The type comes from the Upper Cretaceous (?Maastrichtian) of Roquefort, Haute-Garonne, France.

MATERIAL STUDIED. BMNH EE6170–72, EE6263–64, MGB 37459, 37543, 37548–49.

REMARKS. This species was originally placed in *Offaster* by Cotteau (1887b) and Lambert (1927), but differs from the type species of that genus, *O. pilula* (Lamarck), in lacking a clear marginal fasciole, as originally pointed out by Lambert when setting up this species. *O. pilula* and *O. leymeriei* both have rather rudimentary aboral pores and have almost no anterior sulcus. We have found that small individuals (<15 mm) have a clearly developed marginal fasciole and that this is largely lost during growth. These small individuals also have a slight anterior sulcus developed from the ambitus adorally, like *O. pilula*.

Cotteau (1887b) erected the species *Offaster leymeriei* on the

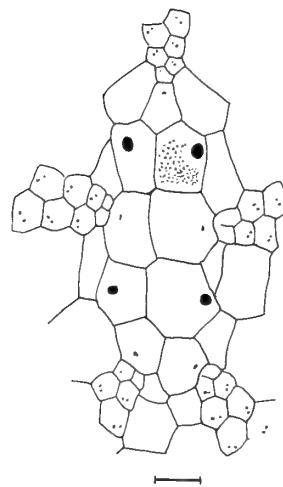


Fig. 14 Camera lucida drawing of plating in *Offaster leymeriei* Cotteau, 1887 from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); MGB 37549, apical disc. Scale bar = 1 mm.

basis of a 30 mm individual from the Upper Cretaceous (?Maastrichtian) of Roquefort, Haute-Garonne, France. Lambert (1927) subsequently erected the species *O. dallonii* from the Maastrichtian of Sapeira, near Tremp, Catalonia. Lambert compared his species with Cotteau's and separated *dallonii* on the grounds that it was smaller, a little less elongate, its lower face less flat, its peristome more anterior and opening not within a depression, but slightly raised, its periproct is slightly higher and its ambulacral plates are less tall and the pore-pairs are more closely spaced. We have not been able to study Cotteau's type material, but suspect that the differences cited by Lambert are more apparent than real and derive largely from the artistic rendition of the specimens in question. In any case, topotype material of *O. leymeriei* from Roquefort (BMNH E9465) is indistinguishable from our material from both Tremp and Santander.

Genus **CARDIASTER** Forbes, 1850

DIAGNOSIS. Cordiform in outline. Petals distinct, though small, with asymmetric columns, the posterior columns being slightly narrower than the anterior columns. An anterior sulcus runs from apex to peristome, and is deepest at the ambitus. Plastron plating biserial after the initial two or three plates. A marginal fasciole is developed around posterior and lateral parts of the test.

Cardiaster sp.

Pl. 4, fig. 19; Fig. 16

DIAGNOSIS. Test up to 40 mm in length, width about 85% of length, cordiform in outline with distinct anterior groove; tapering to a blunt point posteriorly. Upper surface with median ridge and sloping sides; disc plating not preserved in either specimen. Petals flush; columns of pore-pairs unequal, with posterior series better developed than anterior series pores. Pore-pairs not joined by conjugate groove and the two pores are angled to each other. Peristome slightly depressed, kidney-shaped. Plastron broad, with biserial plating following a triangular labral plate. Periproct posterior. Fascioles not present around the anterior margin; elsewhere, test preservation too abraded to tell. Larger aboral tubercles lie along the margins of the anterior groove and a few are also present adapically.

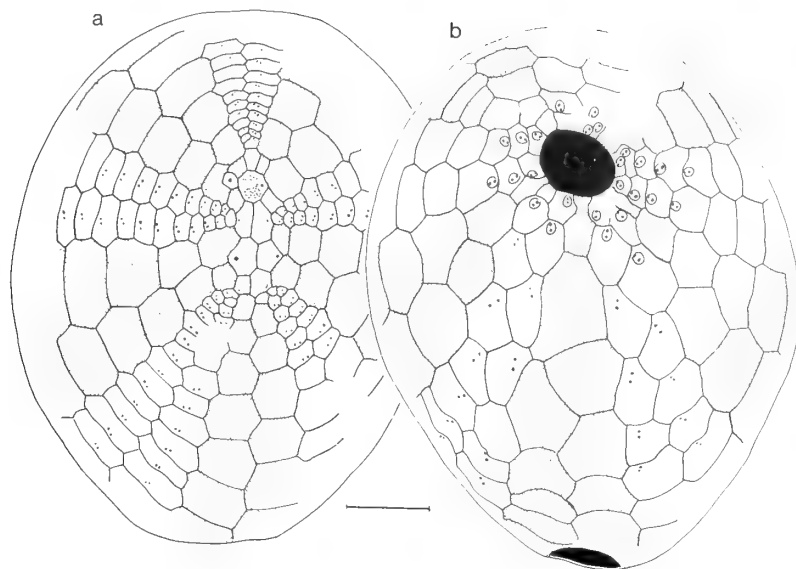


Fig. 15 Camera lucida drawing of plating in *Offaster leymeriei* Cotteau, 1887 from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria). BMNH EE6170. **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

OCCURRENCE. Upper Thanetian of Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE6174–75.

REMARKS. Although both specimens are incomplete, the cordiform outline and distinctive plastron plating are indicative of just two holasteroid taxa, *Cardiaster* or *Pseudholaster*. *Cardiaster* has the labral plate and first sternal plate arranged uniserially, whereas *Pseudholaster* has the labral plate extending to touch the outer edge of the second labral plate. Furthermore, *Cardiaster* has a marginal fasciole that disappears towards the anterior, whereas *Pseudholaster* has no fascioles whatsoever. Unfortunately, preservation is so poor that the presence or absence of a marginal fasciole towards the posterior of the test cannot be confirmed. Plastron plating, however, is more decisive, in that the labral plate appears to be short and well separated from the second sternal plate. For this reason we assign the specimens to *Cardiaster*.

Our specimens differs from the common Maastrichtian *Cardiaster granulosus* (Goldfuss) in having a wider plastron with plates in each column extending less far towards the opposite ambulacrum. It also lacks enlarged primary tubercles running up the aboral surface of the anterior interambulacra, which are characteristic of *C. granulosus*.

Genus *HEMIPNEUSTES* L. Agassiz, 1836

DIAGNOSIS. Test cordate with flat base and domed upper surface. Apical disc elongate with four gonopores; madrepores typically extend over the anterior two genital plates. Paired ambulacra petaloid with petal columns strongly unequal, the posterior column of pore-pairs always being very much better developed. The anterior petals are flexed strongly to the anterior. Frontal groove distinct from apex to peristome, with sharp, but not keeled, margins. Periproct posterior, with test indented immediately beneath periproct so that the opening is just visible from below. Plastron composed of cuniform alternating plates that extend almost across the full width of the plastron. No fascioles.

Hemipneustes striatoradiatus (Leske, 1778)

Pl. 7, figs 3, 4

- 1778 *Spatangus striato-radiatus* Leske: 104, pl. 14, fig. A.
- 1855 *Holaster striato-radiatus* d'Orbigny: 113, pls 802, 803.
- 1875 *Hemipneustes leymeriei* Hébert: 594, pl. 20.
- 1892 *Hemipneustes leymeriei* Hébert; Nicklès: 110.

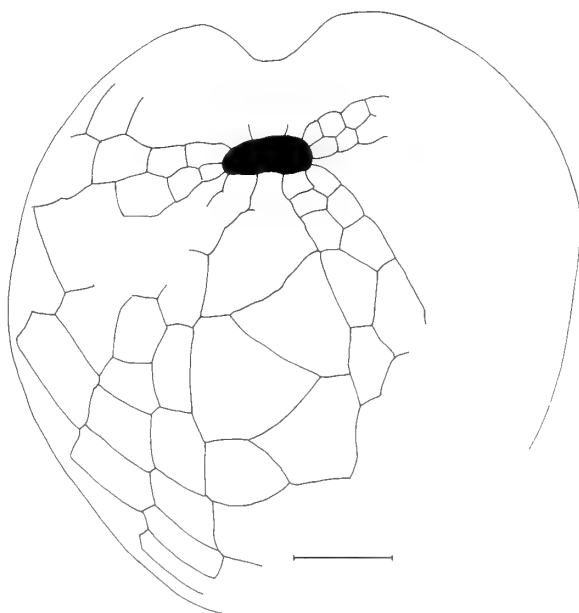


Fig. 16 Camera lucida drawing of plating in *Cardiaster* sp. from the late Thanetian of Casas de Oraien (Navarra); BMNH EE6174, oral surface. Scale bar = 5 mm.

- 1907 *Hemipneustes leymeriei* Hébert; Lambert: 709.
 1935 *Spatangoides striatoradiatus* Leske; Smiser: 71, pl. 8, fig. 1.
 1973 *Hemipneustes leymeriei* Hébert; Radig: 13.
 1987 *Hemipneustes striatoradiatus* Leske; Van der Ham *et al.*: 32, pl. 18, fig. 2.
 1995 *Hemipneustes striatoradiatus* Gallemí *et al.*: table 1.

DIAGNOSIS. Test 66 mm in length; tall (height 75% of length); oval in outline and only slightly longer than wide. Upper surface strongly domed in both lateral and posterior profiles. Anterior sulcus narrow and sharply defined at the ambitus.

OCCURRENCE. Maastrichtian, horizon 4, Olazagutia Pass, Navarra province. ?Maastrichtian, horizon 2, Santander.

MATERIAL STUDIED. BMNH EE6179, MGB 37442–43.

REMARKS. Only three specimens of this species were found along with the very much more common *H. pyrenaicus* Hébert at Olazagutia Pass. They are easily distinguished from that species by their domed profile and very much more circular outline.

Fragments of a rather tall, domal *Hemipneustes* are found in the lower beds at Santander. Unfortunately, these are too incomplete to be certain of their specific identity.

***Hemipneustes pyrenaicus* Hébert, 1875** Pl. 7, figs 1, 2

- 1875 *Hemipneustes pyrenaicus* Hébert: 593, pl. 19.
 1892 *Hemipneustes arnaudi* Cotteau: 165, pl. 21, figs 3, 4.
 1892 *Hemipneustes pyrenaicus* Hébert; Nicklès: 110.
 1907 *Hemipneustes pyrenaicus* Hébert; Lambert: 709.
 1920 *Hemipneustes pyrenaicus* Hébert; Lambert: 25.
 1973 *Hemipneustes pyrenaicus* Hébert; Radig: 57, pl. 8, figs 6–9, pl. 9, figs 1–4.
 1992 *Hemipneustes pyrenaicus* Hébert; Gallemí: 244, photo 13.
 ?1996 *Hemipneustes pyrenaicus* Hébert; Wilmsen *et al.*: 354.

DIAGNOSIS. Test up to 95 mm in length; elongate, with width 75–80% of length; height 60–65% of length; subquadrate in profile with slight peak centrally. Ambulacral groove narrow; apical disc central to a little anterior. Periproct opening on inward-sloping portion of test and thus just visible in oral view.

OCCURRENCE. Maastrichtian, beds 2–4, Olazagutia Pass, Navarra province; Maastrichtian, Somo Beach near Santander, Cantabria province; Lower Maastrichtian, Homes Morts Member, Salàs de Pallars, Tremp Basin, Catalonia (Gallemí 1977).

MATERIAL STUDIED. BMNH EE4381, EE6180–87, MGB 37472, 37474–75, 37477.

REMARKS. Readily distinguished from *H. striatoradiatus* by its more elongate form, more inwardly sloping posterior face and more depressed profile.

***Hemipneustes* sp.**

- 1992 *Hemipneustes leymeriei* Gallemí: 240, photo 12.

DIAGNOSIS. Test longer than 80 mm (damaged at rear, but probably approximately 90 mm); rounded, almost circular with width very probably representing 90–95% of length; height around 55% of length; subrectangular in profile with a slight depression centrally where the apical system lies. Ambulacral groove narrow at the ambitus and expanding moderately towards the frontal part of the apical surface. Periproct unknown.

OCCURRENCE. Maastrichtian, horizon 4, Santander. Homes Morts Member, Lower Maastrichtian, Salàs de Pallars, Tremp Basin (Gallemí, 1992).

MATERIAL STUDIED. MGB 37533.

REMARKS. Distinguished from *H. pyrenaicus* and *H. striatoradiatus* by its rounded, almost circular form and from the latter species also by its more depressed, flat-topped profile.

Family ECHINOCORIDAE Lambert, 1917

Genus ECHINOCORYS Leske, 1778

DIAGNOSIS. Test hemispherical to subconical with flat base; no frontal groove. Apical disc central; holasterid in form with four gonopores; madrepores confined to genital plate 2. Peristome D-shaped and downward facing; test generally slightly depressed towards opening. All ambulacra similar, non-petaloid; pore-pairs small and double aborally. Periproct transverse; on lower surface. Plastron meridosternous. No fascioles.

REMARKS. *Echinocorys* has been divided into a large number of species on the basis of overall shape. Although individual morphologies can be very distinctive and of great use for local correlation, there is also a great deal of integradation amongst forms, with similar extremes of shape recurring at different times in the history of the group. As there are no structural differences in the form of the test, we here assign all forms to one large species complex, *E. scutata* Leske, and recognize the various shape varieties as named forms.

***Echinocorys scutata* Leske, 1778**

- 1778 *Echinocorys scutata* Leske: 111, pl. 15, figs a, b.

DIAGNOSIS. Ambulacral plates becoming low and densely packed adapically; aboral pore-pairs small and circumflexed, becoming denser adapically, but not conjugate and not forming distinct petals.

***Echinocorys scutata* forma *ovata* Leske, 1778** Fig. 17a

- 1778 *Echinocorys ovatus* Leske: 178, pl. 53, fig. 3.
 1801 *Anachytes ovatus* Lamarck: 347.
 1903 *Echinocorys ovatus* Leske; Lambert: 69, pl. 4, figs 6, 7, pl. 5, figs 1, 2.

DIAGNOSIS. Test up to 90 mm in length and ovate in outline; width approximately 75–85% of length. Subconical in profile, varying from flat-topped to distinctly pointed. Height 67–80% of length. Ambitus low and a little depressed towards the peristome. Aboral pore-pairs small and circumflexed; becoming more crowded adapically, but not forming distinct petals and never conjugate.

OCCURRENCE. Maastrichtian, horizon 3, Santander, Cantabria; Lower Maastrichtian, black-shale facies, Sarasate, motorway section, Navarra.

MATERIAL STUDIED. BMNH EE4567, BMUW 94788, 95005, 95006, 95014, 94780, 94787, 94786, 95012–13, 94783, 94788, 94996–98, 94791.

***Echinocorys scutata* forma *belgica* Lambert, 1898**

Fig. 17b

- 1829 *Anachytes sulcatus* Goldfuss: 146 (pars), pl. 45, fig. 1a–c only.
 1898b *Echinocorys belgicus* Lambert: 43, pl. 4, figs 9, 10.
 1903 *Echinocorys belgicus* Lambert; Lambert: 80.
 1996 *Echinocorys belgicus* Lambert; Wilmsen *et al.*: 354.

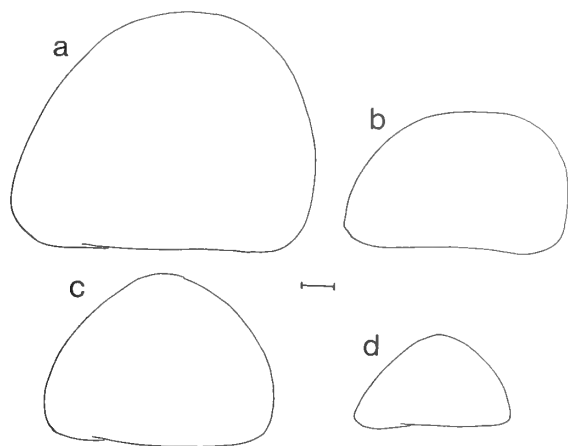


Fig. 17 Outlines of tests of *Echinocorys scutata* Leske in lateral profile (anterior to the right). **a**, forma *ovata* Leske, 1778, BMNH EE6194, Maastrichtian of Santander, Cantabria. **b**, forma *belgica* Lambert, 1898, BMNH EE6193, Maastrichtian of Santander. **c**, forma *cotteau* Lambert, 1903, BMNH EE6191, Late Thanetian of Casas de Oraien, Navarra. **d**, forma *pyrenaica* Seunes, 1888, BMNH EE6192, Danian of Erice, Navarra.

DIAGNOSIS. Test 62 mm in length and 58 mm in width (width 94% of length); ovate, with rounded anterior and slightly pointed posterior. Height 35 mm (56% of length); with broad, rather flat, upper surface, steeply sloping anterior and more gently sloping posterior. Ambitus very low. Lower surface distinctly sunken inside margins. Petals small and non-conjugate; becoming denser towards apex.

OCCURRENCE. Maastrichtian, level 5, Santander.

MATERIAL STUDIED. BMNH EE6194.

REMARKS. Distinguished from other forms by its wide, subcircular outline and depressed lateral profile.

***Echinocorys scutata* forma *pyrenaica* Seunes, 1888**

Fig. 17d

1888a *Echinocorys pyrenaicus* Seunes: 814, pl. 30, fig. 5, pl. 31, fig. 2.

1927 *Echinocorys obliquus* [Nilsson MS] Ravn: 336, pl. 4, fig. 2, pl. 5, fig. 2.

DIAGNOSIS. Small form up to 50 mm in length; width 85–90% of length; ovate and slightly pointed posteriorly. Flat base with sharp and low ambitus. Upper surface conical in lateral and posterior profile; height approximately 50% of test length. Periproct on oral surface. Aboral pore-pairs small; becoming more closely-spaced adapically.

OCCURRENCE. Danian *Coraster* Beds, Erice, Navarra. Also known from the Danian of Alfás del Pi, Alicante, Spain. The type of *obliquus* comes from the Upper Danian of Denmark.

MATERIAL STUDIED. BMNH EE6192, MGB 37323.

REMARKS. The strongly conical profile and sharp ambitus distinguish this form from all others.

***Echinocorys scutata* forma *cotteau* Lambert, 1903**

Pl. 4, figs 20–22, Pl. 7, figs 5, 6; Fig. 17c

1847 *Ananchytes semiglobus* Goldfuss; Agassiz & Desor: 136 (pars).

1856 *Echinocorys vulgaris* Breynius; Leymerie & Cotteau: 343.

1877 *Echinocorys semiglobus* Goldfuss; Cotteau: 62, pl. 5, figs 14–18.

1887b *Echinocorys semiglobus* Goldfuss; Cotteau: 662.

1890 *Echinocorys semiglobus* Goldfuss; Seunes: 194.

1903 *Echinocorys cotteau* Lambert: 84, pl. 4, fig. 8.

1907 *Echinocorys cotteau* Lambert; Lambert: 718.

DIAGNOSIS. Test small, up to 70 mm length only; width 85–95% test length, ovate in outline. Test low conical in profile, height 65–73% of test length. Ambulacra simple and identical, with pore-pairs becoming moderately dense towards the apex, but remaining small and semi-colon-like; no clearly defined petaloid area. Peristome slightly wider and perioral area more depressed, forming characteristic rounded anterior rim.

OCCURRENCE. Upper Thanetian. Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE4530–4534, EE6189–91, MGB 37403–37405, 37429–37432.

REMARKS. Differs from forma *belgica* in profile; that form being very much more flat topped. Less conical and with a more rounded ambitus than forma *pyrenaica*.

Genus *JERONIA* Seunes, 1888

DIAGNOSIS. Ovate in outline with domed upper surface and flat base; distinctly pointed at posterior. Apical disc holasterid, with three gonopores (genital plate 2 without a gonopore). Aboral pore-pairs small and insignificant, placed centrally towards lower edge of ambulacral plates and not crowded or enlarged adapically. Peristome ovate and downward-facing; rather strongly depressed; oval. Periproct inframarginal, opening on posterior projection. Tuberculation generally fine, but with prominent band of very large primary tubercles around the ambitus. Plastron plating meridosternous; very narrow.

REMARKS. Similar to *Echinocorys* in shape, but with a stronger sternal keel and distinct posterior point, and with a supra-ambital band of large tubercles around the posterior of the test.

***Jeronia pyrenaica* Seunes, 1888**

Figs 18–20

1888a *Jeronia pyrenaica* Seunes: 810, text-figs 1–3, pl. 30, fig. 1.

?1889 *Offaster cuneatus* Seunes: 806, pl. 24, fig. 3.

1891 *Jeronia pyrenaica* Seunes: 29, text-figs 4, 5, pl. 3, figs 1, 2.

1975 *Jeronia pyrenaica* Seunes; Plaziat *et al.*: 634, fig. 10.

DIAGNOSIS. As for genus. In both specimens which show the apical disc plating genital plate 2 has only madrepores and no gonopore, as first illustrated by Seunes (1891).

OCCURRENCE. Near base of chalk facies; Upper Danian, Larumbe; basal Thanetian, *G. angulata* Zone (ZB 5), Aristregui, Navarra province.

MATERIAL STUDIED. BMNH EE6195, MGB 37353, 37382–37383.

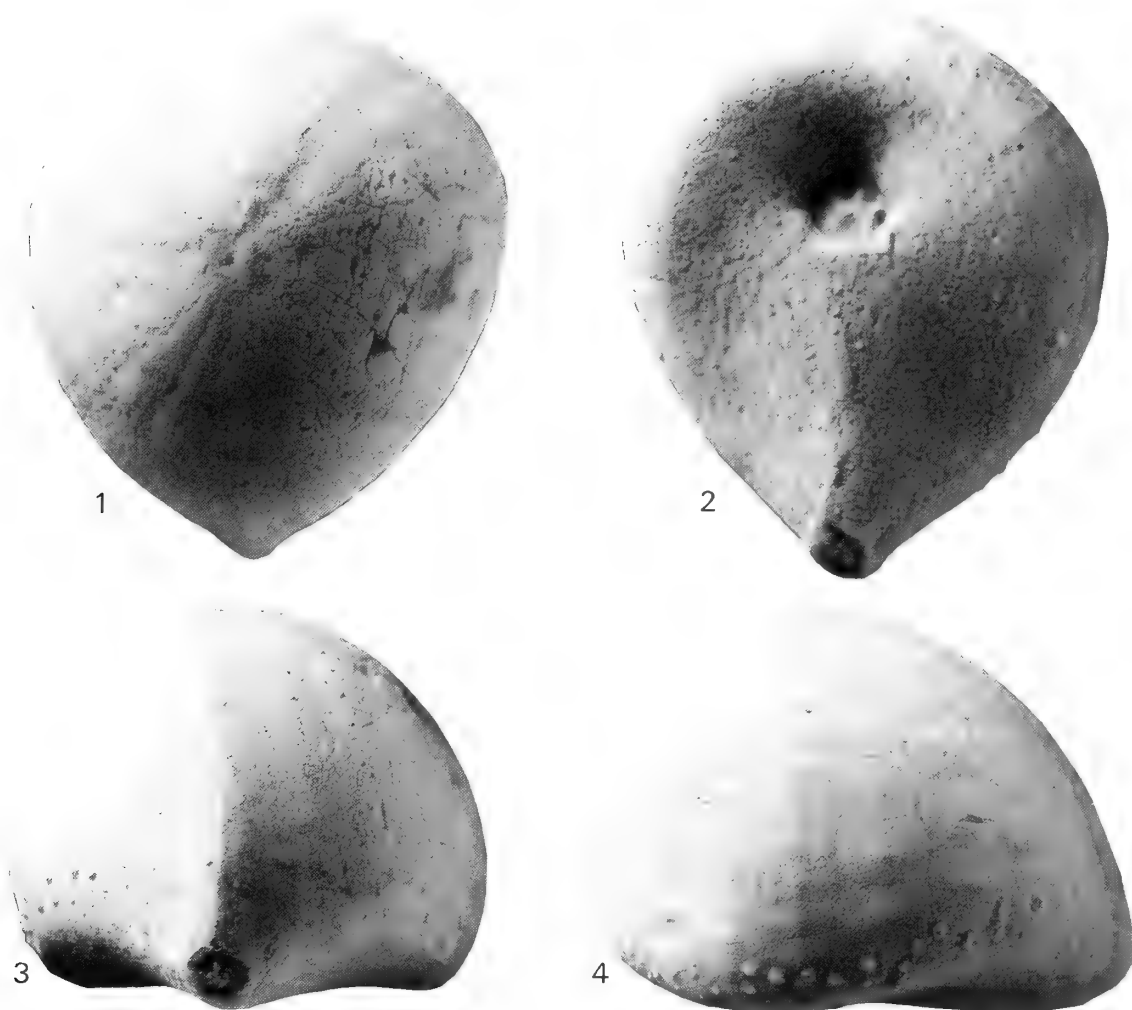


Fig. 18 *Jeronia pyrenaica* Seunes, 1888, from the late Danian of Larumbe (Navarra); MGB 37382, **1**, apical surface; **2**, oral surface; **3**, posterior profile; **4**, lateral profile. All $\times 1.5$.

Family STEGASTERIDAE Lambert, 1917

DIAGNOSIS. Test cordate, with prominent frontal groove from the ambitus to the peristome. Apical disc holasterid with four gonopores. Paired ambulacra with subpetaloid to rudimentary pore-pairs. Phyllode pore-pairs lacking from around peristome. Plastron orthosternous without rostral plate. Marginal fasciole may be present, but no other fascioles are developed.

Genus STEGASTER Pomel, 1883

DIAGNOSIS. Thick-tested holasterid with flat base and cordate outline. Frontal groove absent adapically, deepening to ambitus with

sharp keels and continuing as well-defined furrow to mouth. Petals rudimentary, flush. Plastron orthosternous. Periproct on posterior face, just supramarginal with subanal tallon. No fascioles.

Stegaster bouillei (Cotteau, in de Bouillé, 1873)

Pl. 5, figs 1–3; Figs 21, 22

1873 *Holaster Bouillei* Cotteau, in de Bouillé: 450.

1889 *Stegaster bouillei* Seunes: 816, pl. 26, fig. 2.

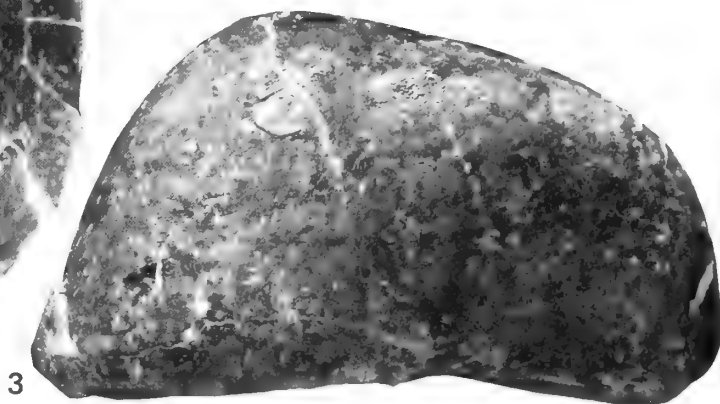
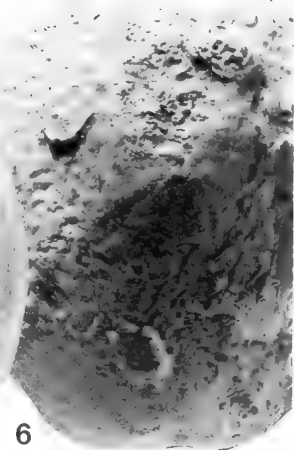
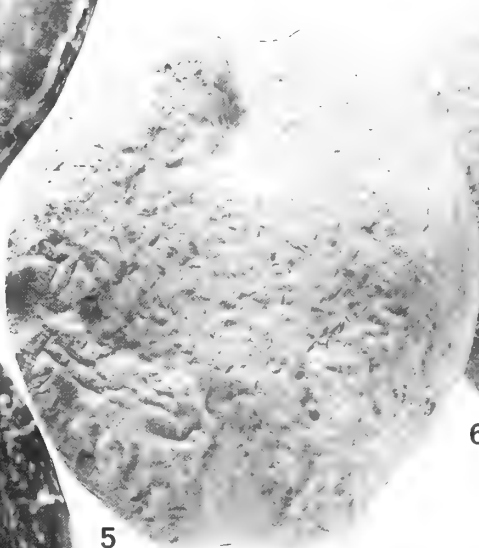
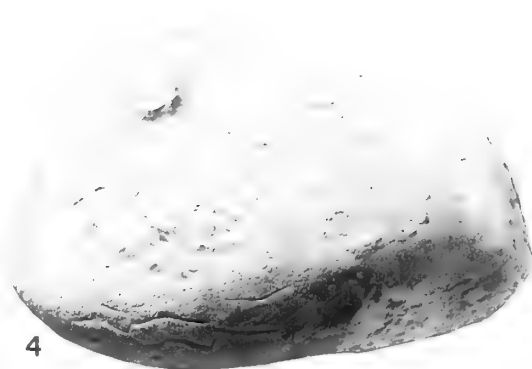
1892 *Stegaster bouillei* Nicklès: 111.

DIAGNOSIS. Test elongate, up to 75 mm in length; tapering to posterior truncation. Width about 90% of length. In profile subconical with tallest point anterior; height about 50–60% of length. Anterior

PLATE 5

Figs 1–3 *Stegaster bouillei* (Cotteau, in de Bouillé, 1873), BMNH EE6066, Maastrichtian of Sarasate, Navarra. Oral, apical and lateral views, $\times 1$.

Figs 4–6 *Stegaster palaeocenicus* sp. nov., MGB 37351 (**holotype**), Danian of Aristregui, Navarra. Lateral, oral and aboral views, $\times 1$.



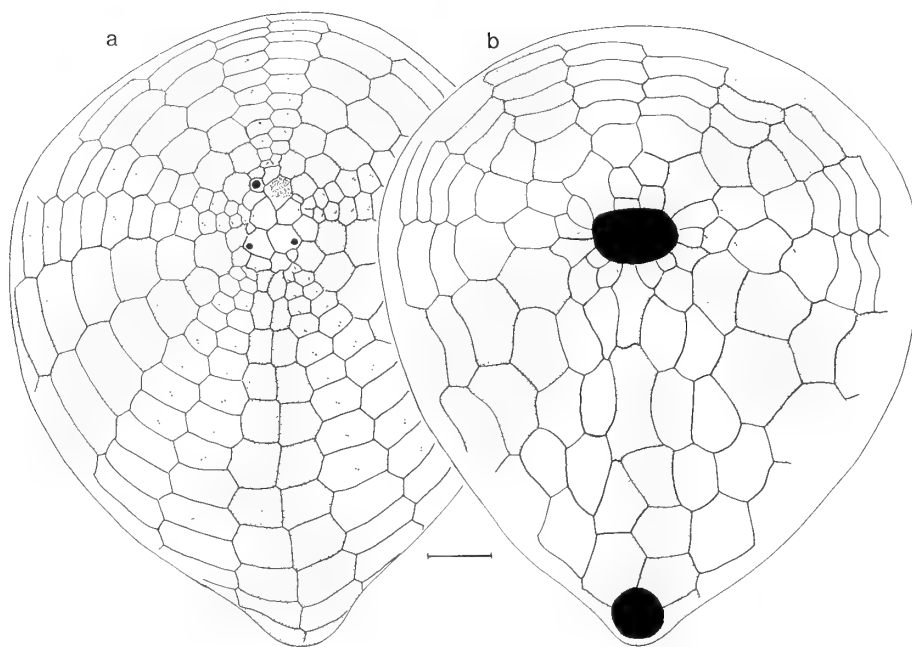


Fig. 19 Camera lucida drawings of plating in *Jeronia pyrenaica* Seunes, 1888, from the late Danian of Larumbe (Navarra); MGB 37382, **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

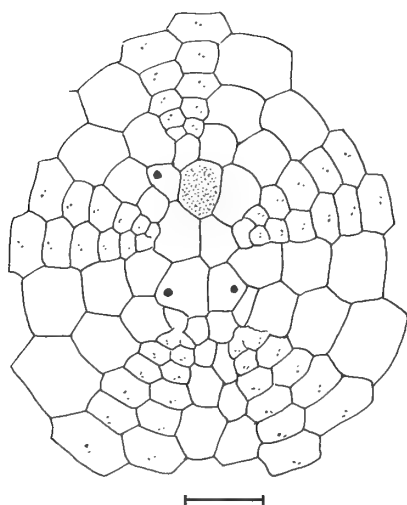


Fig. 20 Camera lucida drawing of plating in *Jeronia pyrenaica* Seunes, 1888 from the late Danian of Aristregui (Navarra); MGB 37353, apical disc. Scale bar = 5 mm.

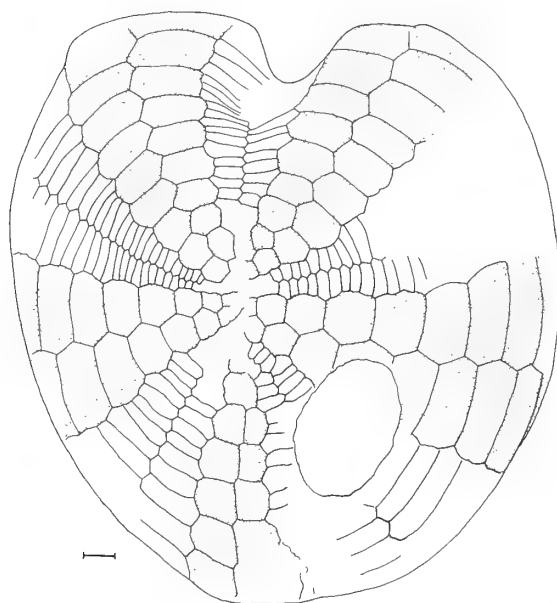


Fig. 21 Camera lucida drawing of plating in *Stegaster bouillei* (Cotteau, in de Bouillé, 1873) from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74753, apical surface (interambulacra shaded). Scale bar = 5 mm.

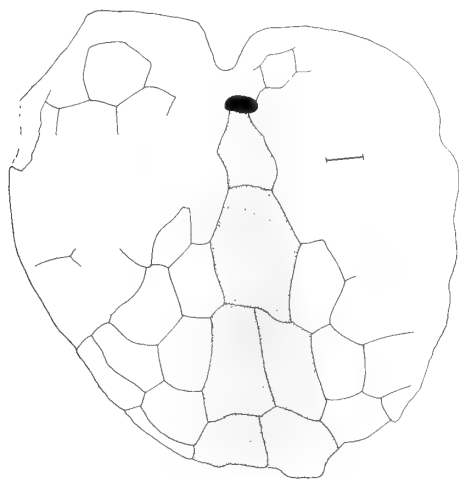


Fig. 22 Camera lucida drawing of plating in *Stegaster bouillei* (Cotteau, in de Bouillé, 1873) from the late Maastrichtian of Bidart (Pyénées-Atlantiques, France); BMUW 94988, oral surface (interambulacra shaded). Scale bar = 5 mm.

sulcus sharp and well developed, forming obvious narrow groove on oral surface. Ambulacral plates low and relatively wide, compared to *S. altus*, and with elongate pore-pairs en chevron. Larger primary tubercles present close to the apex and along the posterior ridge between the apex and periproct. Larger tubercles also developed just above the ambitus around the posterior part of the test. Periproct supra-ambital, but test depressed below the periproct so that the periproct opening is just visible in oral view.

OCCURRENCE. Lower Maastrichtian (black shale facies), Sarasate, Navarra; upper Upper Maastrichtian, Bidart, Pyénées-Atlantiques, France. The species was first described from the Maastrichtian of the French Pyrenees between Gan and Rébénac, and is also known from the Province of Alicante, Spain and from Turkey, Crimean peninsula, Republic of Georgia, and the North Caucasus.

MATERIAL STUDIED. BMNH EE4375, EE4568, EE4566, EE6066, MGB 37286–87, 37300.

REMARKS. Easily separated from *S. altus* by its characteristic elongate shape and vaulted upper surface with the tallest point anterior. *S. cotteui* differs in having a disjunct plastron and a more ovate outline.

Stegaster altus Seunes, 1889

- 1889 *Stegaster altus* Seunes: 815, pl. 26, fig. 1.
 1891 *Stegaster chalmasi* Seunes: 23, pl. 1, fig. 1.
 1892 *Stegaster chalmasi* Seunes; Nicklès: 110.
 1892 *Stegaster altus* Seunes; Nicklès: 111.
 1995 *Stegaster novoi* Lambert; Gallemí et al.: 269, table 1.

DIAGNOSIS. Test up to 50 mm in length. Like *S. bouillei*, but test almost as wide as long and very tall; height more than 70% of test length. Ambulacral plates much taller than in *S. bouillei*.

OCCURRENCE. Lower Maastrichtian (black shale facies), Sarasate, Navarra. Upper Upper Maastrichtian, Bidart, Pyénées-Atlantiques, France. This species was first described from the Maastrichtian of

the French Pyrenees. It also occurs in the Alicante Province of Spain and in Tunisia, Turkey, Bulgaria, Republic of Georgia and the North Caucasus.

MATERIAL STUDIED. BMNH EE4396, EE4347–50, EE6176–78, MGB 37298–99, BMUW 74610, 74753, 74788, 74945, 94946, 94949, 94988, 94994.

REMARKS. Readily distinguished from other species of *Stegaster* by its wider and much taller test.

Stegaster cotteui Seunes, 1889

Pl. 6, figs 1–5; Figs 23, 24

1889 *Stegaster cotteui* Seunes: 813, pl. 25, fig. 3.

DIAGNOSIS. Test up to 60 mm in diameter; cordiform, as wide as long or slightly wider. All material crushed, but apparently rather rounded at the ambitus when not crushed and not very tall; tallest point anterior of mid-length. Ambulacral plates rather tall with small, almost rudimentary pore-pairs. Plastron disjunct with labral plate separated from succeeding sternal plate by ambulacral plates. Tuberculation unknown.

OCCURRENCE. Upper Upper Maastrichtian, Bidart, Pyénées-Atlantiques, France.

MATERIAL STUDIED. BMNH 75697, E2916, E10972, BMUW 74603, 74607, 74609a, 74772, 74789, 74791, 94946, 94948, 94985, 94986, 94989, 94991a.

REMARKS. Most similar to *Stegaster heberti*, differing primarily in having a disjunct plastron (a feature which we can confirm is not size-related). It comes very close to *Sanchezaster habanensis* Lambert in appearance, differing only in having double pores on ambulacral plates rather than single pores.

Stegaster palaeocenicus Smith & Gallemí, sp. nov.

Pl. 5, figs 4–6; Fig. 25

DIAGNOSIS. *Stegaster* with disjunct plastron and postero-lateral interambulacra.

DESCRIPTION. Test up to 55 mm in length; ovate with slight anterior invagination and small bilobed posterior projection in aboral plan view. Distinctly conical in profile with tallest point coincident with apical disc; rounded in front and sloping to rear. Frontal groove absent apically, but rapidly deepening at the ambitus and continuing as a deep channel to the peristome, which is forward-facing. The interambulacral plates on either side form a distinct keel. Apical disc positioned anteriorly (about 30% test length from the anterior border); elongate and of standard holasterid structure with four gonopores. Aboral pore-pairs small and sunken; never elongate; becoming microscopic away from the apical disc. Plastron orthosternous and disjunct, with ambulacral plates separating the labrum and first sternal plate. The latero-posterior interambulacra are also disjunct. Periproct supra-ambital, on short posterior face and above small double protuberance. Aboral tuberculation composed of a uniform scattering of small tubercles set in a dense granulation; no enlarged tubercles differentiated. No marginal fasciole.

OCCURRENCE. Late Danian of Aristregui and Larumbe, Navarra Province.

TYPES. Holotype MGB 37351, paratypes MGB37352, 37381.

REMARKS. The deep sulcus developed from the ambitus to the peristome identifies this as a stegasterid. Our species lacks the marginal fasciole and enlarged tubercles of *Guettaria* and *Rispolia*.

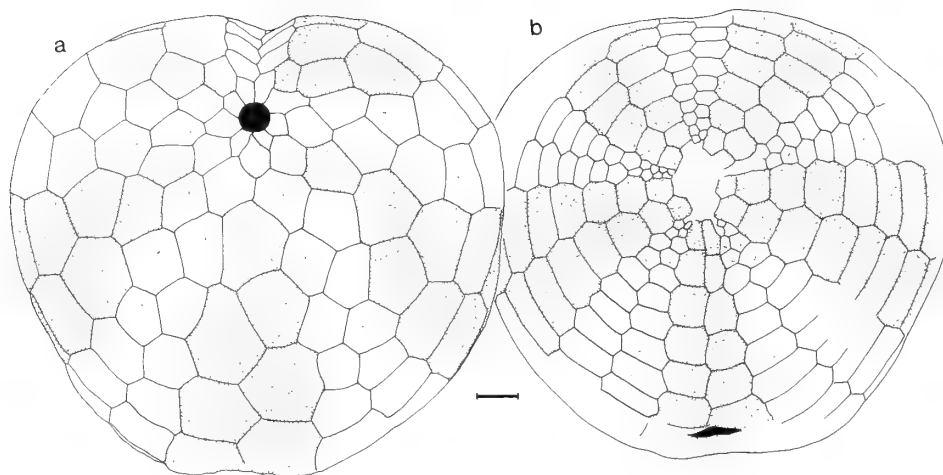


Fig. 23 Camera lucida drawings of plating in *Stegaster cotteui* Seunes, 1889, from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74603, **a**, oral surface; **b**, apical surface (interambulacra shaded). Scale bar = 5 mm.

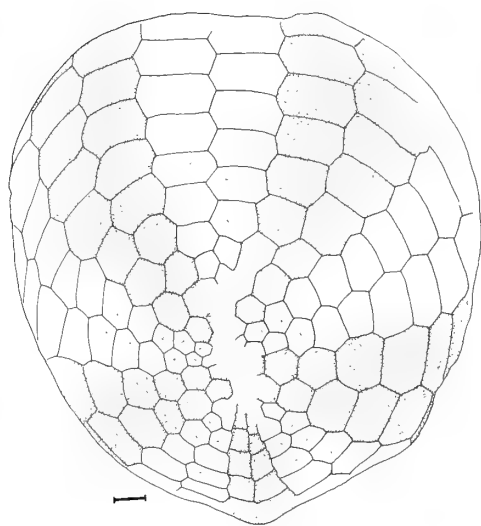


Fig. 24 Camera lucida drawing of plating in *Stegaster cotteui* Seunes, 1889, from the late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 74792, apical surface (interambulacra shaded). Scale bar = 5 mm.

and its disjunct plastron distinguishes it from all but three species of *Stegaster*, *S. cotteui* Seunes, *S. charlesi* Lambert and *S. mairei* Lambert, all Maastrichtian in age. In none of these are the latero-posterior interambulacra interrupted as they are in our species. *S. mairei* further differs in being subglobular in shape with its periproct positioned much higher. *S. cotteui* has a much narrower anterior sulcus, more anterior peristome (10% test length from the anterior rather than almost 30%) and is more depressed in profile. *S. charlesi* resembles our species in profile, but, according to Lambert (1931: M7), has such a reduced labral plate that only ambulacral plates surrounding the peristome. Unfortunately the only plating diagram of *S. charlesi* (Lambert 1931: M5, fig. 3) gives insufficient detail and we have not examined Lambert's type to confirm this very unusual plate arrangement.

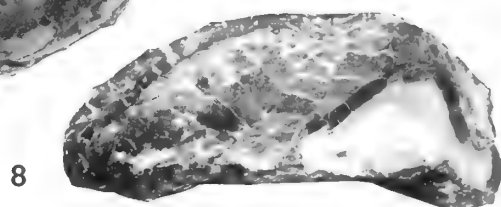
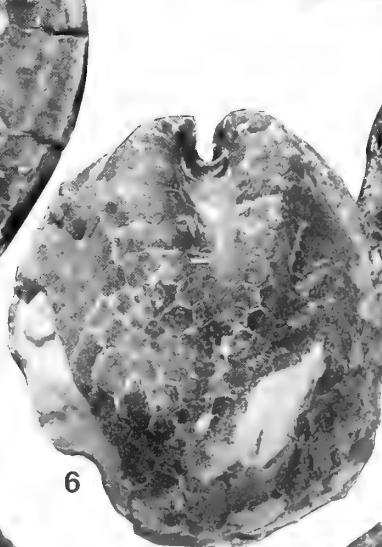
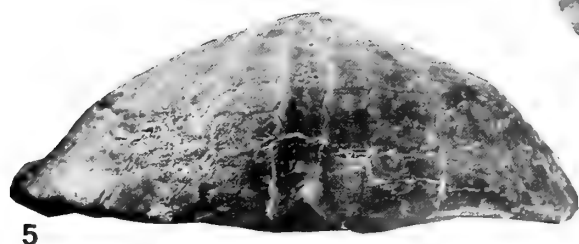
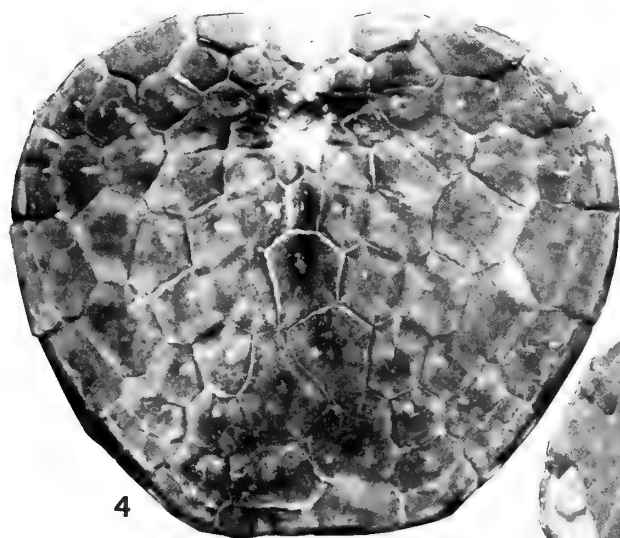
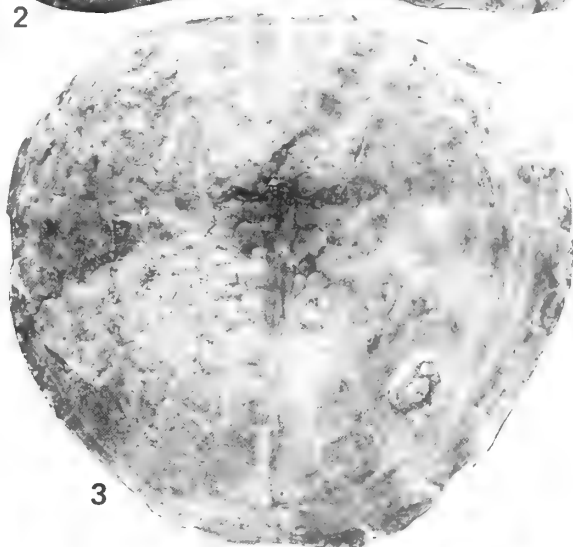
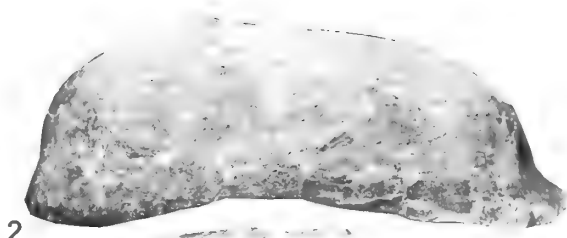
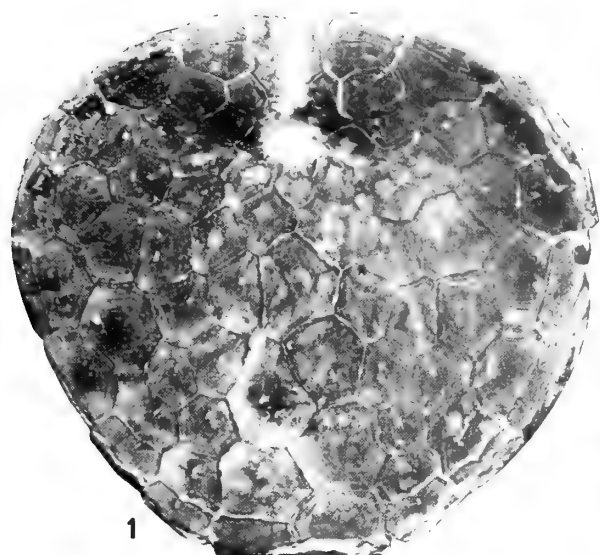
Genus *THOLASTER* Seunes, 1891

DIAGNOSIS. Test elongate with very deep frontal groove at ambitus and adorally; tapering to posterior truncation. Apical disc with four genital plates each with a gonopore. Aboral pore-pairs rudimentary, ambulacra flush. Frontal groove with sharp lateral carina; developed from apex to peristome. Oral surface flat. Plastron orthosternous. Periproct on posterior face. Very large primary tubercles prominent towards apex and along the aboral margins of the frontal groove. No fascioles.

PLATE 6

Figs 1–5 *Stegaster cotteui* Seunes, 1889, Upper Maastrichtian of Bidart, Pyrénées-Atlantiques, France. **1–3**, BMUW 74603, oral, lateral and apical views, $\times 1$. **4, 5**, BMUW 94985, oral and lateral views, $\times 1$.

Figs 6–8 *Tholaster munieri* (Seunes, 1889), BMUW 94993, Upper Maastrichtian of Bidart, Pyrénées-Atlantiques, France. Apical, oral and lateral views, $\times 1$.



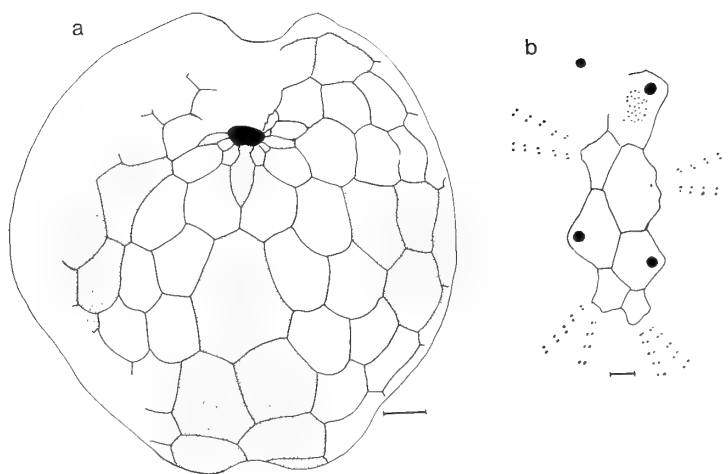


Fig. 25 Camera lucida drawings of plating in *Stegaster palaeocenicus* sp. nov. from the late Danian of Aristregui (Navarra); **a**, holotype MGB 37351, oral surface (interambulacra shaded); **b**, paratype MGB 37352, apical disc. Scale bars: **a** = 5 mm; **b** = 1 mm.

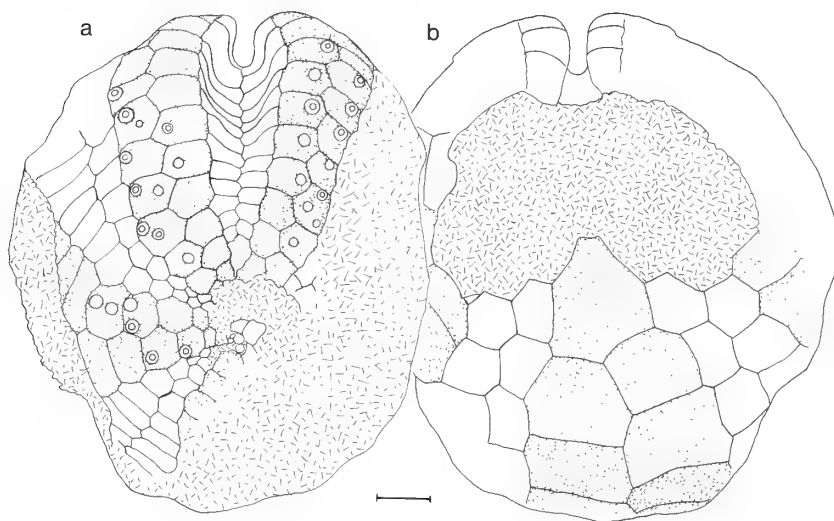


Fig. 26 Camera lucida drawings of plating in *Tholaster munieri* (Seunes, 1889) from the late Late Maastrichtian of Bidart (Pyrénées-Atlantiques, France); BMUW 94993, **a**, apical surface; **b**, oral surface. Interambulacra shaded. Scale bar = 5 mm.

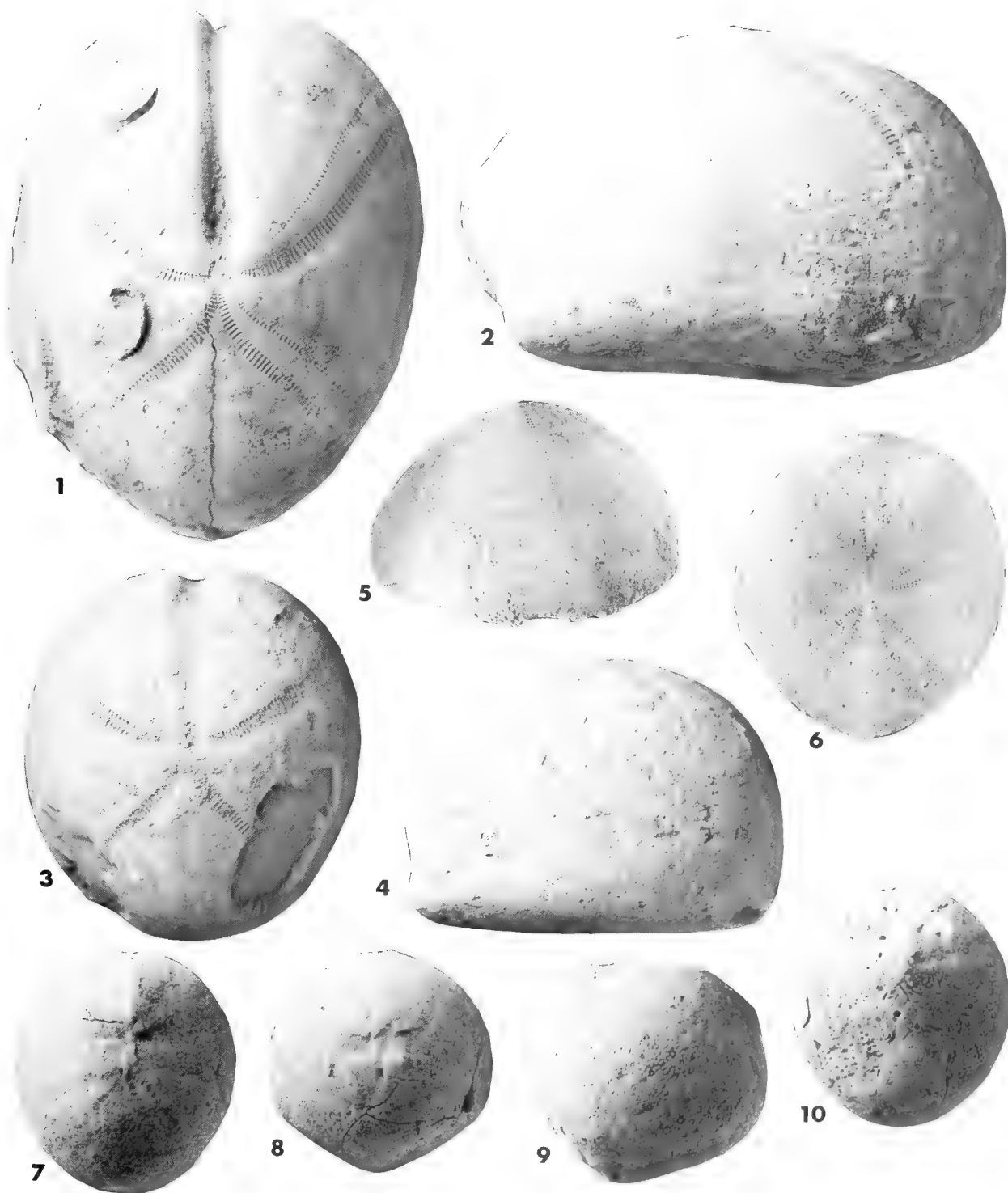
PLATE 7

Figs 1, 2 *Hemipneustes pyrenaicus* Hébert, 1875, BMNH EE6180, Maastrichtian of Olazagutia Pass, Navarra. Apical and lateral views, $\times 1$.

Figs 3, 4 *Hemipneustes striatoradiatus* (Leske, 1778), BMNH EE6179, Maastrichtian of Olazagutia Pass, Navarra. Apical and lateral views, $\times 1$.

Figs 5, 6 *Echinocorys scutata* forma *cotteaui* Lambert, 1903, BMNH EE6190, Thanetian of Casas de Oraien, Navarra. Lateral and apical views, $\times 1$.

Figs 7–10 *Pseudoffaster caucasicus* (Dru, 1884), BMNH EE6234, Maastrichtian of Sarasate, Navarra. Apical, posterior, lateral and oral views, $\times 2$.



Tholaster munieri (Seunes, 1889)

Pl. 6, figs 6–8; Fig. 26

1889 *Gibbaster munieri* Seunes: 819, pl. 27, fig. 1.1891 *Tholaster munieri* Seunes: 23.

DIAGNOSIS. As for genus. Test up to 45 mm in length; slightly longer than wide. Both specimens crushed and height unknown.

OCCURRENCE. Upper Upper Maastrichtian, Bidart, Pyrénées-Atlantiques, France. The type comes from the Maastrichtian of the same region (Lasseube) and it has been recorded from several other localities in the Department of Landes, France.

MATERIAL STUDIED. BMUW 74768, 94993.

REMARKS. The long, deep frontal groove and prominent primary tubercles make this a very easily recognizable species.

Genus *PSEUDOFFASTER* Lambert, in Lambert & Thiéry, 1924

DIAGNOSIS. Test ovate with anterior sulcus present only below the ambitus. Ambulacra composed of tall plates with rudimentary pores. Apical disc holasterid, with four gonopores. Periproct high on steep posterior face. Peristome small, facing forwards and opening into anterior sulcus. Marginal fasciole present.

Pseudoffaster caucasicus (Dru, 1884) Pl. 7, figs 7–10;

Fig. 27

1884 *Offaster caucasicus* Dru: 514, pl. 26, figs 5–10.1927 *Pseudoffaster caucasicus* (Dru); Lambert: 42.

DIAGNOSIS. As for genus. Test 20.3 mm in length, ovate in outline; width approximately 90% of length; widest approximately midlength. Height 90% of length, with strongly convex lower surface and tallest point immediately anterior of the apical disc.

OCCURRENCE. Maastrichtian of Sarasate, Navarra, Spain. Also recorded from the Lower Maastrichtian Areny Sandstone of Tremp, Catalonia, Spain, by Lambert (1927).

MATERIAL STUDIED. BMNH EE6234.

Genus *GALEASTER* Seunes, 1889

DIAGNOSIS. Test ovate with shallow anterior sulcus persisting to the peristome. Tall, vaulted upper surface and keeled lower surface. All ambulacra with tall plates and rudimentary pores. Apical disc holasterid, with four gonopores; anterior pair of genital plates generally fused. Periproct high on steep posterior face. Plastron orthosternous. Peristome small, facing forwards and opening into anterior sulcus. Subanal fasciole present.

Galeaster bertrandi Seunes, 1889

Pl. 4, figs 14–18; Fig. 28

1889 *Galeaster bertrandi* Seunes: 822, pl. 27, figs 2, 3.

DIAGNOSIS. Test length 11.1 mm, width 9.0 mm, height 9.4 mm. Weakly cordiform and tapering to a point posteriorly; very tall in profile with tallest point towards the posterior, sloping anteriorly and with vertically truncate posterior. Lower surface strongly convex with keeled posterior interambulacrum. Shallow anterior sulcus from a little above the ambitus to the peristome. Apical disc plating elongate, with small gonopores just apparent at this size. Ambulacral plates very tall with pore-pairs centrally placed; pores double throughout.

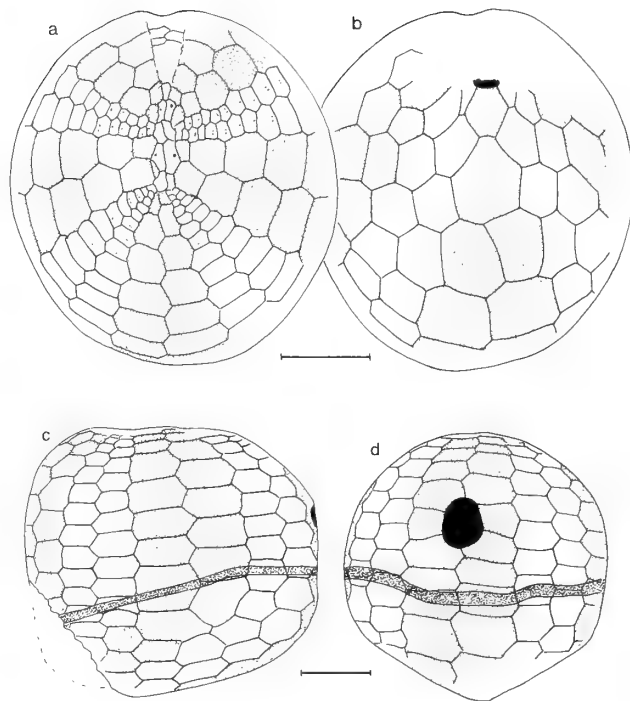


Fig. 27 Camera lucida drawings of plating in *Pseudoffaster caucasicus* (Dru, 1884) from the Maastrichtian of Sarasate (Navarra); BMNH EE6234. **a**, apical surface; **b**, oral surface; **c**, lateral profile; **d**, posterior profile. Interambulacra shaded. Scale bar = 5 mm.

OCCURRENCE. Maastrichtian, horizon 2, Santander. The type of this species was reported from the 'Garumnian' (?Maastrichtian) of the Pyrénées-Atlantiques, France.

MATERIAL STUDIED. BMNH EE6188.

REMARKS. Unfortunately, we have only a single specimen of this interesting species. The very anterior mouth, opening into the frontal groove immediately distinguishes this species from *Offaster*, whose mouth is downward-facing and not opening into an anterior sulcus. Amongst holasteroids only *Galeaster* possesses a subanal fasciole, orthosternous plating and a distinct frontal sulcus. However, the apical disc has the two anterior genital plates fused in *Galeaster*, according to Poslavskaya & Moskvina (1960), whereas our specimen undoubtedly has a suture separating genital plates two and three. We do not know what the apical disc plating in Seunes' type material is like.

Order SPATANGOIDA Claus, 1876

DIAGNOSIS. Ovate to heart-shaped with compact apical disc with four genital plates. Posterior interambulacral plates differentiated to form a plastron adorally. Aboral ambulacra typically with pore-pairs enlarged and forming petals; often depressed.

Family MICRASTERIDAE Lambert 1920

DIAGNOSIS. Apical system ethmophract; plastron mesamphisternous. Aboral tuberculation consisting of larger primary tubercles dispersed amongst a dense groundmass of fine granules.

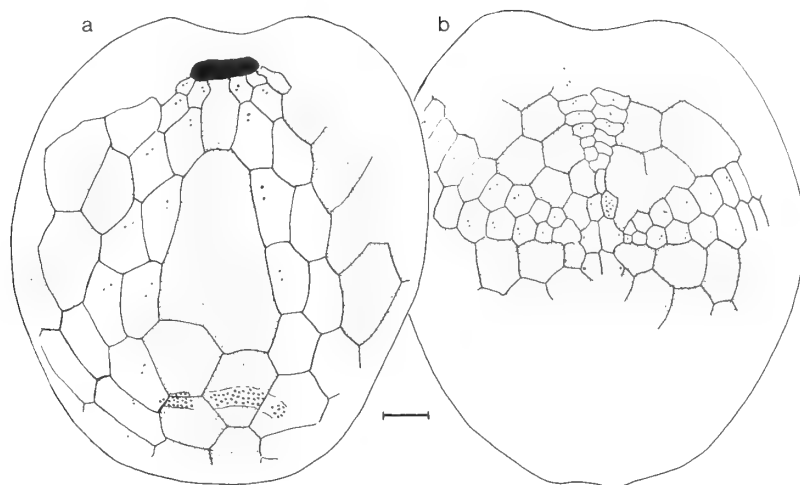


Fig. 28 Camera lucida drawings of plating in *Galeaster bertrandi* Seunes, 1889, from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); BMNH EE6188, **a**, oral surface, interambulacra shaded; **b**, apical surface. Scale bar = 1 mm.

Genus **MICRASTER** Agassiz, 1836

Subgenus **ISOMICRASTER** Lambert, 1901

DIAGNOSIS. Test cordate, with shallow anterior sulcus; subconical in profile with periproct very low on short posterior face. Apical disc ethmophract with four gonopores. Anterior ambulacrum sunken with pore-pairs similar to those of other ambulacra. Peristome forward-facing and placed almost at the anterior border, largely hidden in oral view by the projecting labral plate. No subanal fasciole.

REMARKS. The forward facing peristome and strongly labiate labral plate ally this lineage with the type species, *M. coranguinum* Leske. It is distinguished, however, by its lack of a subanal fasciole and by the highly conical profile of the test.

***Micraster (Isomicraster) stolleyi* Lambert, 1901**

1869 *Epiaster gibbus* Schlüter: 237, pl. 2, figs 1, 1a–c.

1901 *Isomicraster stolleyi* Lambert, in Lambert 1895a–1901a: 959.

1927 *Isomicraster dallonii* Lambert; Lambert: 48.

1975 *Micraster stolleyi* Lambert; Stokes: 79, fig. 30f.

1989 *Micraster (Isomicraster) aff. stolleyi* Lambert; Kuchler & Kutz: 196, text-fig. 2.

1992 *Micraster stolleyi* Lambert; Gallemí: 335, figs 88–90.

DIAGNOSIS. As for genus. Test approximately 70 mm in length and 45 mm in height.

OCCURRENCE. ?Uppermost Campanian–?Lower Maastrichtian; Erice, Navarra, Spain.

MATERIAL STUDIED. MGB 37304.

REMARKS. This unique specimen is crushed, but cannot be mistaken for any other species. It comes from the upper beds in the shale-limestone succession immediately underlying the Danian *Coraster* Limestones at Erice. This has been determined as Upper Campanian – lowermost Maastrichtian (Kuchler & Kutz, 1989).

Subgenus **PSEUDOGIBBASTER** Moskvina, 1983

DIAGNOSIS. Test cordate, with shallow anterior sulcus; inflated, with vertically truncated posterior. Apical disc ethmophract with four gonopores. Anterior ambulacrum sunken with pore-pairs differentiated from those of other ambulacra. Peristome almost non-labiate and downward-facing. Subanal fasciole present.

REMARKS. The non-labiate peristome differentiates this from the type species, *M. coranguinum* Leske, and from all Upper Maastrichtian species of *Micraster* from north-western Europe. It is distinguished from *Isaster* and *Cyclaster* in having four gonopores rather than three.

***Micraster (Pseudogibbaster) tercensis* Cotteau, 1863**

Pl. 8, figs 8–12; Figs 29, 30

1856 *Micraster brevis* (Desor); Leymerie & Cotteau: 346.

1863b *Micraster cortestudinarium* Goldfuss; Cotteau: 220 (55).

1863b *Micraster tercensis* Cotteau: 221 (56).

1877 *Micraster tercensis* Cotteau; Cotteau: 69, pl. 7, figs 29–32.

1975 *Micraster tercensis* Cotteau; Plaziat *et al.*: 640, fig. 10.

DIAGNOSIS. Test up to 65 mm in length, with distinct anterior groove; tapering to a blunt point posteriorly. Width 100–110% of length. In profile, subconical with rounded base and approximately vertical posterior truncation. Apex subcentral to slightly anterior; generally a little sunken. Petals moderately long and straight; open-ended distally; anterior pair extending 70% of the radial distance to the margin, posterior pair extending only 55–65% of the distance. Petals depressed with both pores slightly elongate. Anterior ambulacrum with enlarged pores adapically (18–22 enlarged pore-pairs), forming a shallow groove to the peristome. Labral plate moderately long and narrow; sternal plates unequal, with left sternal plate having a smaller contact surface with the labral plate than the right sternal plate. Periproct small, rounded, positioned high on the posterior face. No peripetalous fasciole. Aboral tuberculation consisting of a scattering of larger primary tubercles set amongst a dense uniform groundmass of miliaries. Subanal fasciole present, enclosing four or five enlarged subanal pore-pairs.

OCCURRENCE. Upper Thanetian, *G. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. BMNH EE4514–21, EE6196–6201, MGB 37402, 37426–28.

Genus **CYCLASTER** Cotteau, in Leymerie & Cotteau, 1856

DIAGNOSIS. Micrasterids with three gonopores (no gonopore present on genital plate 2); commonly showing sexual dimorphism in the size of gonopores. Petals short and weakly depressed only; anterior ambulacrum with differentiated pore-pairs adapically. Peristome weakly labiate and downward-facing. Subanal fasciole present; peripetalous fasciole absent or present – when present it may be partial or complete.

Cyclaster gindreii (Seunes, 1888) Pl. 8, figs 1–5; Fig. 31b 1888a *Isopneustes gindreii* Seunes: 795, pl. 28, fig. 2.

DIAGNOSIS. Test up to 35 mm in length. Subquadrate in outline, with width 75–80% of length; widest where anterior petals reach the ambitus and tapering slightly posteriorly to a truncate posterior. Anterior margin uniformly rounded, or with feeble anterior depression in largest individuals. Petals short and well-defined; anterior pair diverging at 110–120°, posterior pair diverging at about 50° and slightly curved. Anterior and posterior petals similar in length, with 16 pore-pairs in 5 mm long petals. The posterior interambulacrum is raised as a keel aborally, and in profile forms the highest part of the test.

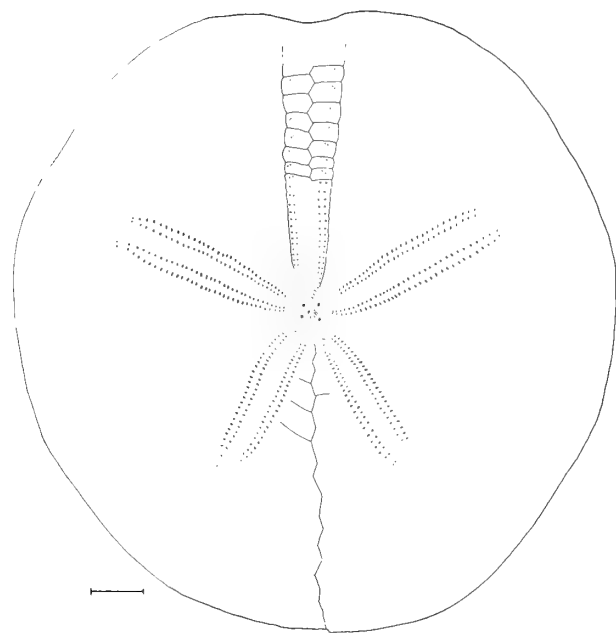


Fig. 29 Camera lucida drawing of plating in *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, from the late Thanetian of Casas de Oraien (Navarra); BMNH EE4521, apical surface. Scale bar = 5 mm.

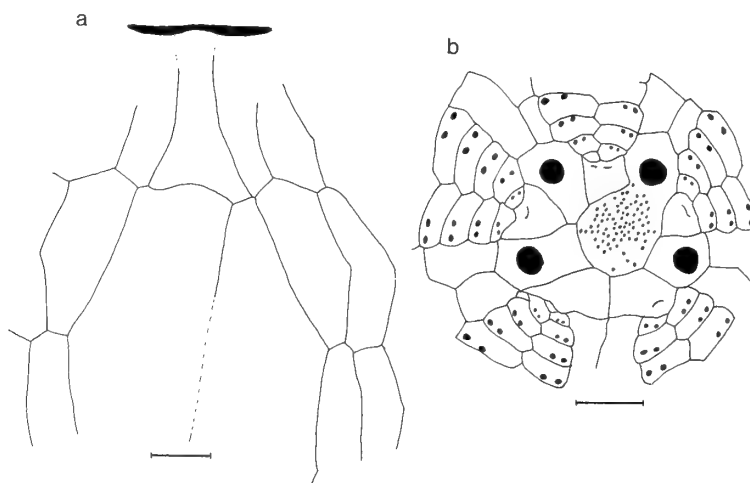


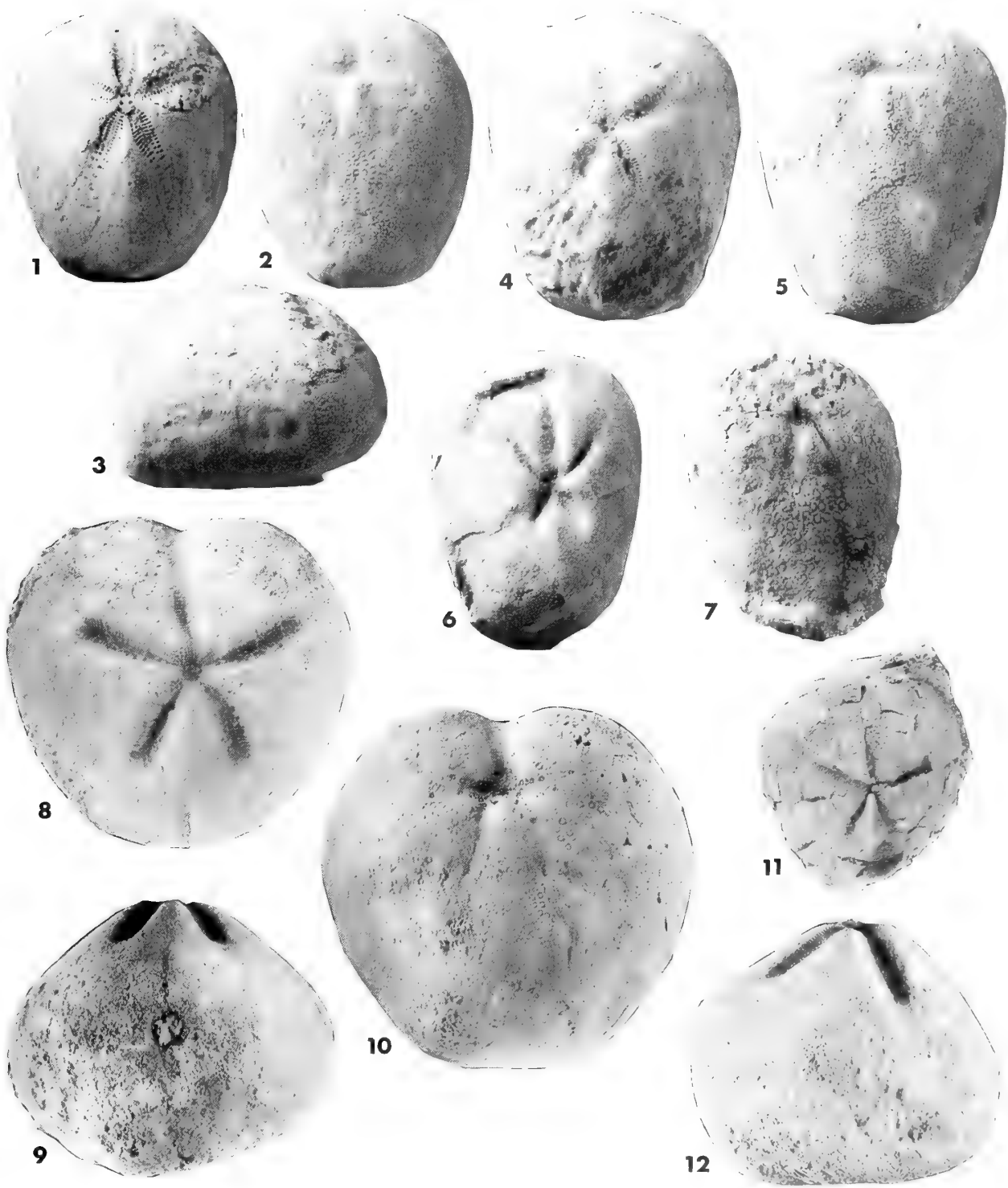
Fig. 30 Camera lucida drawings of plating in *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, from the late Thanetian of Casas de Oraien (Navarra); a, BMNH EE6200, adoral interambulacrum 5, peristome at the top; b, BMNH EE4521, apical disc. Scale bars: a = 5 mm; b = 1 mm.

PLATE 8

Figs 1–5 *Cyclaster gindreii* (Seunes, 1888), Danian of Erice, Navarra. **1–3**, BMNH EE6206, apical, oral and lateral views, $\times 1.5$. **4, 5**, BMNH EE6207, apical and oral views, $\times 2$.

Figs 6, 7 *Cyclaster heberti* (Nicklès, 1892), MGB 37551, Maastrichtian of Santander, Cantabria. Apical and oral views, $\times 2$.

Figs 8–12 *Micraster (Pseudogibbaster) tercensis* Cotteau, 1863, Thanetian of Casas de Oraien, Navarra. **8, 9, 12**, BMNH EE4521, apical, posterior and lateral views, $\times 1$. **10**, BMNH EE6200, oral view, $\times 1$. **11**, BMNH EE6201, apical view, $\times 1$.



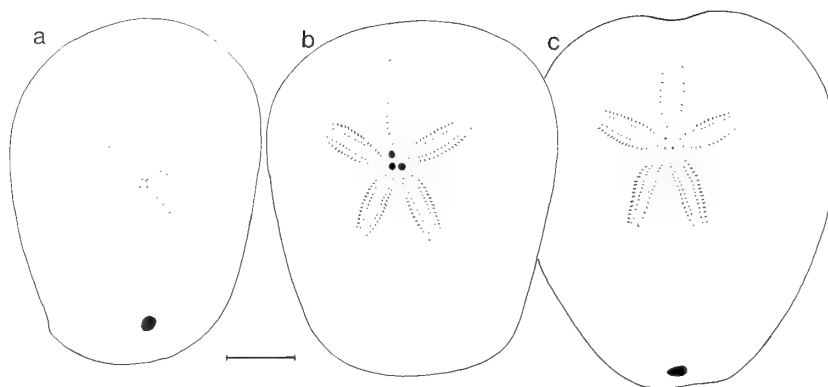


Fig. 31 Camera lucida drawings of plating in *Cyclaster* species. Apical surfaces; **a**, MGB 37551 *C. heberti* (Nicklès, 1892) from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **b**, BMNH EE6206 *C. gindrei* (Seunes, 1888) from the Danian of Erice (Navarra); **c**, BMNH EE6208 *C. aturicus* (Seunes, 1888) from the Danian of Erice (Navarra). Scale bar = 5 mm.

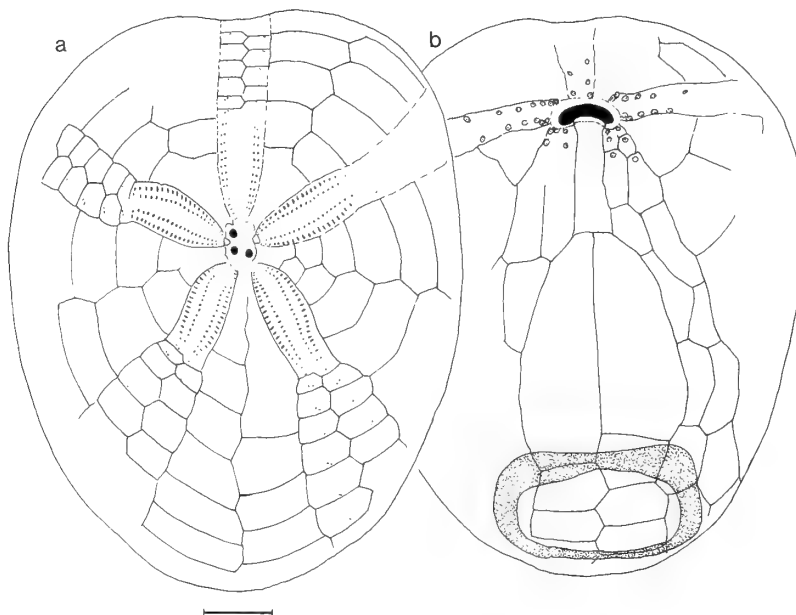


Fig. 32 Camera lucida drawings of plating in *Cyclaster aturicus* (Seunes, 1888) from Astieso hill (Sarasate, Navarra), BMNH EE6068; **a**, apical surface; **b**, oral surface. Scale bar = 5 mm.

PLATE 9

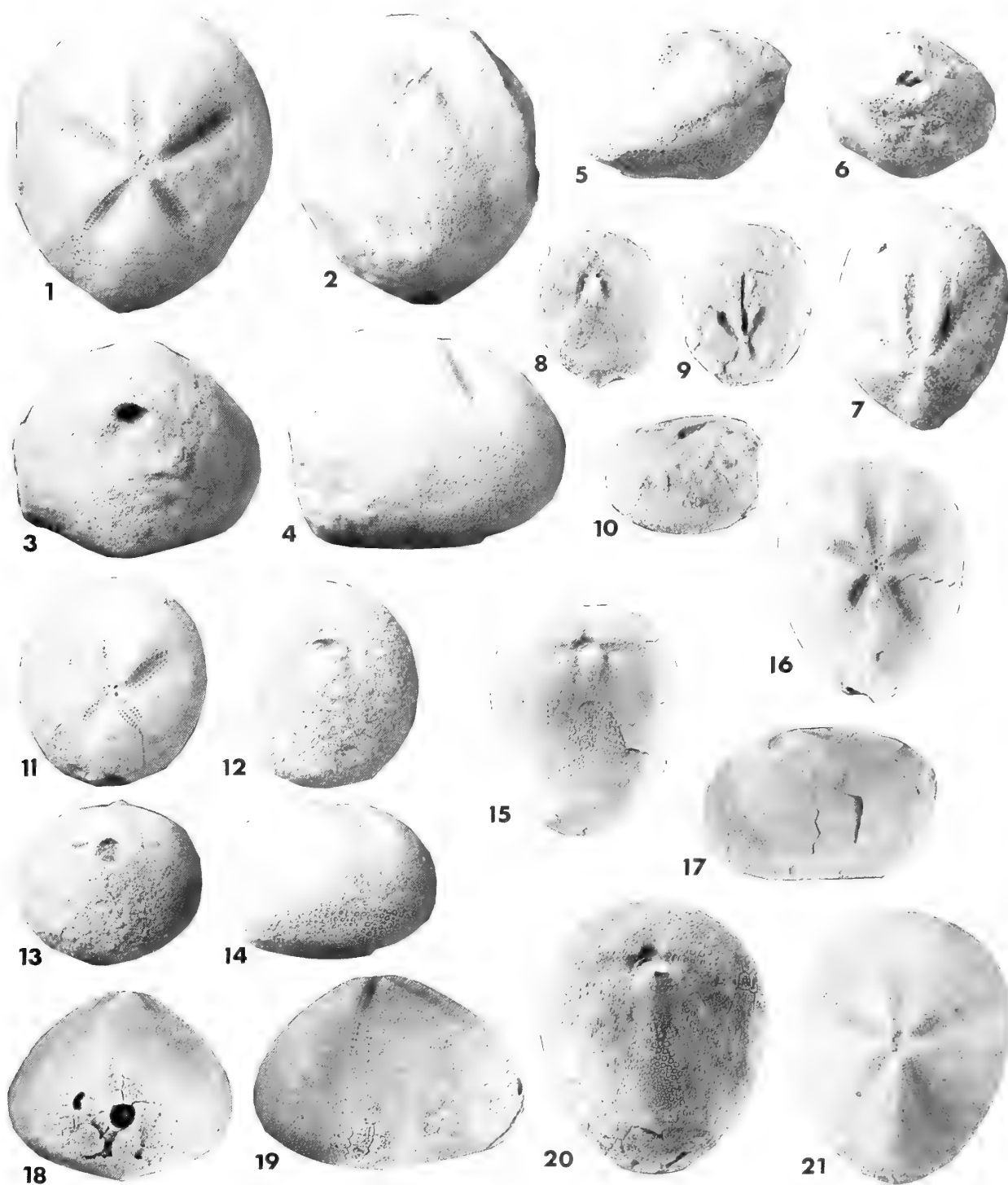
Figs 1–7 *Hemiaster koninckanus* d'Orbigny, 1855. Maastrichtian. **1–4**, BMNH EE6238, Olazagutia Pass, Navarra; apical, oral, posterior and lateral views, $\times 2$. **5–7**, BMNH EE6250, Santander, Cantabria; lateral, posterior and apical views, $\times 2$.

Figs 8–10 *Hemiaster stella* (Morton, 1830), BMNH EE6234, Thanetian of Casas de Oraien, Navarra. Oral, apical and lateral views, $\times 1$.

Figs 11–14 *Hemiaster prunella* (Lamarck, 1816), MGB 37534, Maastrichtian of Santander, Cantabria. Apical, oral, posterior and lateral views, $\times 2$.

Figs 15–17 *Cyclaster aturicus* (Seunes, 1888), BMNH EE6068, Danian of Astieso, Navarra. Oral, apical and lateral views, $\times 1$.

Figs 18–21 *Isaster aquitanicus* (de Grateloup, 1836), BMNH EE6202, Thanetian of Casas de Oraien, Navarra. Posterior, lateral, oral and apical views, $\times 1$.



OCCURRENCE. Danian of Erice, Navarra Province, Spain; Lower Maastrichtian of Tercis, Landes, France.

MATERIAL STUDIED. BMNH EE6206–07, MGB 37305–06, 37319–21, BMUW 95007, 95008, 95009, 96010, 95011, 95019, 95016.

REMARKS. Differs from the rather similar-shaped *Cyclaster heberti* (Nicklès), from the Maastrichtian of Santander, in having much more widely divergent anterior petals and a less parallel-sided outline. Differs from the contemporary *C. aturicus* in being much less cordiform in outline.

***Cyclaster aturicus* (Seunes, 1888)**

Pl. 9, figs 15–17; Figs 31c, 32

1888a *Isopneustes aturicus* Seunes: 797, pl. 28, fig. 3.

DIAGNOSIS. Test up to 35 mm in length; cordiform in outline with the widest point just behind the anterior petals; tapering posteriorly to a truncated point; rounded anteriorly with a distinct anterior sulcus. Width 85–90% of length. Posterior interambulacrum developed as a keel aborally. Anterior and posterior petals similar in length; anterior pair diverging at about 130°, posterior at about 50°; 18 pore-pairs in petals 6.5 mm in length. Patches of dense granulation at the ends of petals and in the posterior interambulacrum, but no continuous fasciole developed.

OCCURRENCE. Danian, Erice and Astieso, Navarra Province, Spain.

MATERIAL STUDIED. BMNH EE6068, EE6208–6209.

REMARKS. This species has the same petal form as *C. gindrei*, with which it co-occurs, but differs from that species in having a wider, more cordiform test.

***Cyclaster heberti* (Nicklès, 1892)** Pl. 8, figs 6, 7; Fig. 31a

1892 *Isopneustes Heberti* Nicklès: 111, pl. 9, figs 12, 13.

1973 *Isopneustes heberti* Nicklès; Radig: 62, pl. 10, fig. 8, pl. 11, figs 1, 2.

1995 *Isopneustes heberti* Nicklès; Gallemí *et al.*: 269, table 1.

DIAGNOSIS. Test up to 25 mm in length (known to reach up to 45 mm elsewhere). Elongate and subquadrate in outline and with very flattened profile; no posterior keel. Test widest at a point immediately behind where the anterior ambulacra reach the ambitus in plan view; rounded in front without any anteal sulcus. Test tapering slightly to posterior truncation. Anterior petals 30–40% longer than posterior petals; diverging at 90° or slightly less. Posterior petals diverging at 45–50°. No peripetalous fasciole developed, even posteriorly, although traces of granulation may be present around the posterior.

OCCURRENCE. Maastrichtian, horizon 6, of Santander, Cantabria, Spain.

MATERIAL STUDIED. MGB37550–51.

REMARKS. Distinguished from the rather similar-shaped *C. gindrei* by the angle of divergence of its anterior petals, and by its lacking a posterior keel. *C. heberti* was first described from El Matet, Alicante Province, Spain. Topotype material from here reaches 45 mm in length and show variable development of the peripetalous fasciole. Most specimens show traces of the fasciole at the base of the posterior petals while some have more continuous fascioles. A few appear to lack any trace of a peripetalous fasciole whatsoever. Our specimens from Santander show no trace of a peripetalous fasciole.

?*Cyclaster* sp.

OCCURRENCE. Maastrichtian, horizon 4, Olazagutia Pass, and Maastrichtian, black shale facies, Sarasate, Navarra Province, Spain.

MATERIAL STUDIED. BMNH EE6210, EE6211.

REMARKS. The specimen from Olazagutia Pass is a large crushed individual, estimated at 35 mm in length and about 30 mm in width. The apical disc is unfortunately lacking, but the test is cordiform with distinct frontal sulcus and short, well-formed, sunken petals. There is a strong subanal fasciole, but no trace of a peripetalous fasciole. The peristome is non-labiate. The style of aboral tuberculation shows this to be a micrasterid, while the lack of a peripetalous fasciole, relatively short petals and non-labiate peristome suggests *Cyclaster*. However, without better material we cannot be sure about its taxonomic placement. It most closely resembles *C. aturicus* (Seunes) in shape.

The specimen from Irurtzun is badly weathered aborally, but is also rather broad and weakly cordate and is similarly only tentatively assigned to *Cyclaster*.

Genus *ISASTER* Desor, 1858

DIAGNOSIS. Ovate micrasterids with weakly conical profile and no frontal sulcus. Apical disc with three gonopores, genital plate 2 lacking a pore. Petals weakly depressed adapically; pore-pairs in all five ambulacra similar. Periproct inframarginal, on inward sloping posterior face. No fascioles.

***Isaster aquitanicus* (de Grateloup, 1836)**

Pl. 9, figs 18–21; Figs 33, 34

1836 *Spatangus aquitanicus* de Grateloup: 176, pl. 2, fig. 17.

DIAGNOSIS. Large tests, up to 65 mm in length, oval in outline and tapering to the posterior. Width 85–95% of length, height 60–70% of length. In profile low domal to subconical with the tallest point coincidental with the apical disc. Apical disc 40–42% test length from anterior; ethmophract. Petals rather short and a little depressed; the two columns being only weakly convergent distally. Anterior paired petals extending only about half the radial distance to the margin, slightly bowed and widely divergent. Posterior petals similar in length to anterior paired petals, but much less divergent. Anterior ambulacrum with enlarged pores in adapical part, which is slightly depressed. This frontal groove is lost towards the ambitus. Peristome kidney-shaped in outline; 20–25% test length from the anterior; downwards facing. Labral plate long and narrow; not projecting over the peristome; sternal plates subequal. Oral surface slightly convex with median part of ridge forming a weak ridge.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain.

MATERIAL STUDIED. 71 specimens, including BMNH EE4522–29, EE6069, EE6202–05, MGB 37406–16, 37433–35.

REMARKS. This is the most common species from Casas de Oraien. One-quarter of our specimens have been bored by predatory gastropods.

Family *HEMIASTERIDAE* Clark, 1917

DIAGNOSIS. Spatangoids with peripetalous fasciole, but no subanal fasciole. Dense uniform aboral tuberculation with few intervening granules.

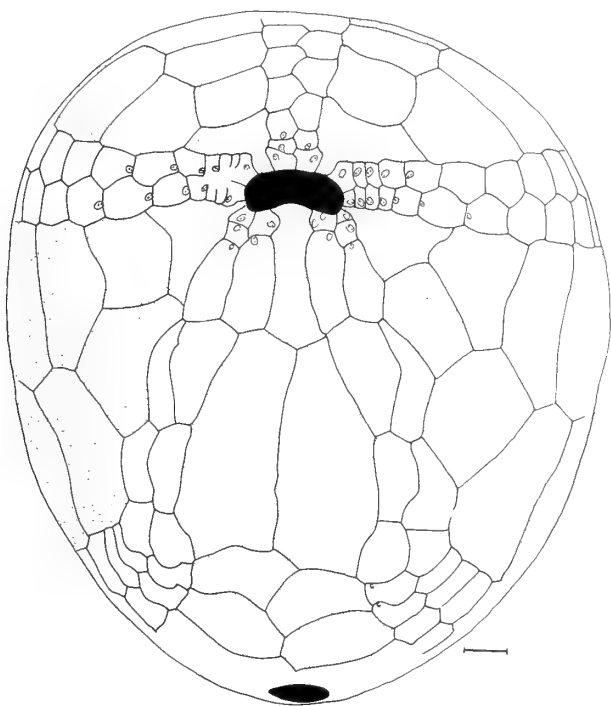


Fig. 33 Camera lucida drawing of plating in *Isaster aquitanicus* (de Grateloup, 1836) from the late Thanetian of Casas de Oraien (Navarra); BMNH EE6202, oral surface. Scale bar = 5 mm.

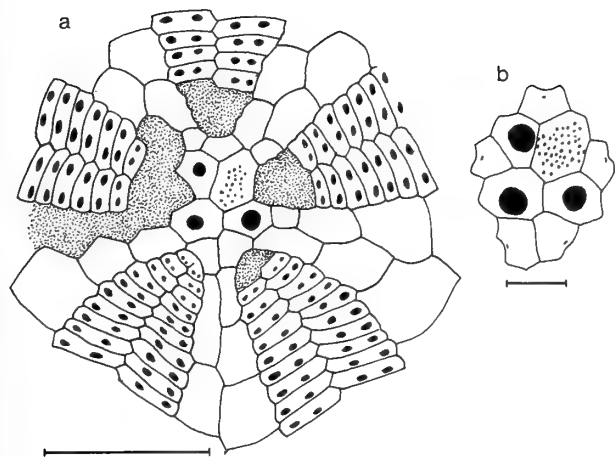


Fig. 34 Camera lucida drawings of plating in *Isaster aquitanicus* (de Grateloup, 1836) from the late Thanetian of Casas de Oraien (Navarra); **a**, BMNH EE6203 apical disc; **b**, BMNH EE6069 apical disc. Scale bars: **a** = 5 mm; **b** = 1 mm.

Genus *HEMIASTER* Agassiz, in Agassiz & Desor, 1847

DIAGNOSIS. Apical disc ethmophract. Anterior sulcus weak or absent.

Hemiaster prunella (Lamarck, 1816)

Pl. 9, figs 11–14; Fig. 35b, c, e

- 1816 *Spatangus prunella* Lamarck: 33.
- 1855 *Hemiaster prunella* Lamarck; d'Orbigny: 242, pl. 881.
- 1856 *Hemiaster prunella* Lamarck; Desor: 122.
- 1927 *Hemiaster prunella* (Lamarck); Lambert: 50.
- 1973 *Hemiaster (Bolbaster) batalleri* Lambert; Radig: 61, pl. 10, figs 4–7.
- 1992 *Hemiaster (Bolbaster) gr. prunella* (Lamarck); Gallemí: 347, 350.
- 1996 *Hemiaster (Bolbaster) prunella* (Lamarck); Wilmsen *et al.*: 354.

DIAGNOSIS. Test up to about 10 mm in length; almost as wide as long; subglobular with weakly domed upper surface; tallest point more or less coincidental with the apical system. In profile, the posterior face is more or less vertical or slopes slightly outwards. Apical disc ethmolytic with four gonopores. Anterior ambulacrum slightly sunken adapically, but becoming flush towards the ambitus; pore-pairs strongly oblique. Anterior petals rather narrow, diverging at *ca.* 110–120°. Posterior petals about half the length of the anterior petals; not strongly bowed. Peripetalous fasciole oval without indentation behind anterior petals. Periproct high on posterior face. Peristome small, kidney-shaped with prominent rim. Labral plate elongate; about half the length of the succeeding sternal plates.

MATERIAL STUDIED. BMNH EE4401–02, EE6240–49, EE6252–61, MGB 37476, 37503, 37515–16, 37518, 37524, 37529, 37534–36, 37538–40, 37547, 37558–59, 37567.

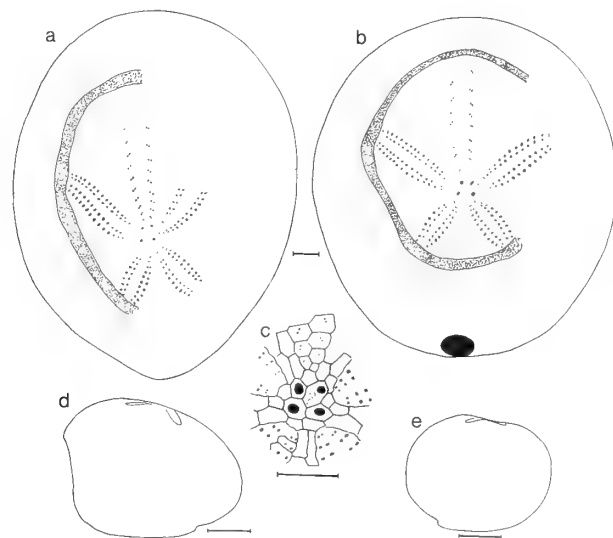


Fig. 35 Camera lucida drawings of plating in *Hemiaster* species. **a, d**, *H. koninckanus* d'Orbigny, 1855; **a**, BMNH EE6250, Maastrichtian, coast west of Cabo Mayor (Santander, Cantabria); apical surface; **d**, BMNH 6238, Maastrichtian, Olazagutia Pass; lateral profile; **b, c, e**, *H. prunella* (Lamarck, 1816); **b**, MGB 37534, apical surface; **c**, BMNH EE6252, apical disc; **e**, BMNH E11093, lateral; **b** and **c** from the Maastrichtian of the coast west of Cabo Mayor (Santander, Cantabria); **e** from the Maastrichtian Maastricht Formation of the Maastricht district, The Netherlands. Scale bars: **a–c** = 1 mm; **d, e** = 5 mm.

OCCURRENCE. Maastrichtian, Santander, Cantabria: horizons 2 (21 specimens), 3 (11 specimens), 4 (13 specimens), 5 (13 specimens), 6 (6 specimens). Maastrichtian, horizons 4 and 5, Olazagutia Pass, Navarra. Lower Maastrichtian, Homes Morts Member, Salàs de Pallars and Sapeira, Tremp area (Gallemí, 1992). Elsewhere this species is known from the Upper Gulpén Formation and Lower and Upper Maastricht Formation, Maastrichtian of the Maastricht district, The Netherlands and Belgium (Van der Ham *et al.*, 1987), and the Maastrichtian of the Mons Basin, Belgium (Smiser, 1935).

REMARKS. Many of the specimens are badly deformed and distorted, making certain identification difficult.

***Hemiaster koninckanus* d'Orbigny, 1855**

Pl. 9, figs 1–7; Fig. 35a, d

- 1855 *Hemiaster koninckanus* d'Orbigny: 250, pl. 885.
 1861 *Hemiaster angustipneustes* Cotteau & Triger: 318, 434, pl. 53, figs 5–11.
 1984 *Hemiaster koninckanus* d'Orbigny, Van der Ham: 169, fig. 1.
 1987 *Hemiaster koninckanus* d'Orbigny, Van der Ham *et al.*: 33, pl. 20, fig. 2.

DIAGNOSIS. Like *H. prunella*, but differing in the following ways: (i) test more elongate, with width 75–85% of test length, rather than almost as wide as long; (ii) in profile, the posterior face is undercut and slopes inwards slightly and the tallest point lies posterior of the apical disc; (iii) the anterior petals are less divergent in smaller individuals, forming an angle of ca. 90–100°; (iv) the labral plate projects slightly more over the peristome.

MATERIAL STUDIED. BMNH E6238–39, EE6250–51.

OCCURRENCE. Maastrichtian, Santander: horizon 2 (5 specimens), horizon 6 (1 specimen). Maastrichtian, horizon 2, Olazagutia Pass, Navarra province. Elsewhere the species is recorded from the Upper Gulpén Formation and Lower and Upper Maastricht Formation, Maastrichtian of the Maastricht district, The Netherlands and Belgium.

***Hemiaster stella* (Morton, 1830)**

Pl. 9, figs 8–10

- 1830 *Spatangus stella* Morton: 245, pl. 3, fig. 11.
 1877 *Hemiaster nasutulus* Sorignet; Cotteau: 65, pl. 6, figs 19, 20.
 1907 *Hemiaster punctatus* var. *garumnica* Lambert: 720 [*nomen nudum*].
 1907 *Hemiaster punctatus* var. *arizensis* Lambert: 721 [*nomen nudum*].
 1975 *Hemiaster garumnicus* Plaziat *et al.*: 643, fig. 10.

DIAGNOSIS. Globose test with convex anterior margin; test slightly longer than wide. Apical disc set a little behind mid-length. Anterior ambulacrum with long parallel-sided frontal groove adapically. An-

terior petals slightly flexuous, diverging at about 80–90°; shorter than anterior sulcus, but about twice as long as posterior petals. Ovate peripetalous fasciole without indentations.

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone, Casas de Oraien, Navarra province, Spain. Also known from the Thanetian of Landes and the Petites Pyrénées, France (Plaziat *et al.*, 1975).

MATERIAL STUDIED. BMNH EE6237.

REMARKS. Differs from *H. koninckanus* and *H. prunella* in the relative length of the anterior and posterior petals, and in the angle of divergence of the anterior pair, which is much more acute than in either of those species.

Family CORASTERIDAE Lambert, in Lambert & Thiéry, 1924

DIAGNOSIS. Paired ambulacra non-petaloid to subpetaloid; more or less flush. Apical system ethmophract. Peristome ovate and downward facing; frontal groove feeble to absent. Peripetalous fasciole only.

Genus CORASTER Cotteau, 1886

DIAGNOSIS. Test globose to ovoid with little or no anterior indentation. Apical disc with four gonopores; test inflated with ambulacral plates relatively tall throughout. Peristome positioned close to the anterior margin and facing forwards.

REMARKS. Distinguished from *Homoeaster* by the much more anterior position of its mouth, and by its proportionally tall ambulacral plates. The peripetalous fasciole of *Coraster* also passes much closer to the apical system posteriorly than is the case in *Homoeaster*. There is considerable variation amongst individuals from the same locality and although many can be placed in one or other of the following species, there is also a good deal of intergradation, making sharp deliniation impossible.

***Coraster vilanovae* Cotteau, 1886**

Pl. 11, figs 4–7; Fig. 37a

- 1886b *Coraster vilanovae* Cotteau: 70, pl. 9, figs 1–4.
 1975 *Coraster vilanovae* Cotteau; Plaziat *et al.*: text-figs 7, 9.
 1995 *Coraster vilanovae* Cotteau; Gallemí *et al.*: 269, table 1.

DIAGNOSIS. Test subglobular; almost as wide as tall with virtually no frontal sulcus.

OCCURRENCE. Danian of Erice, Astieso, Larumbe, Navarra. The type locality is the Danian of Les Foies Blanques, Alfás del Pi, Alicante, Spain (Cotteau, 1886b).

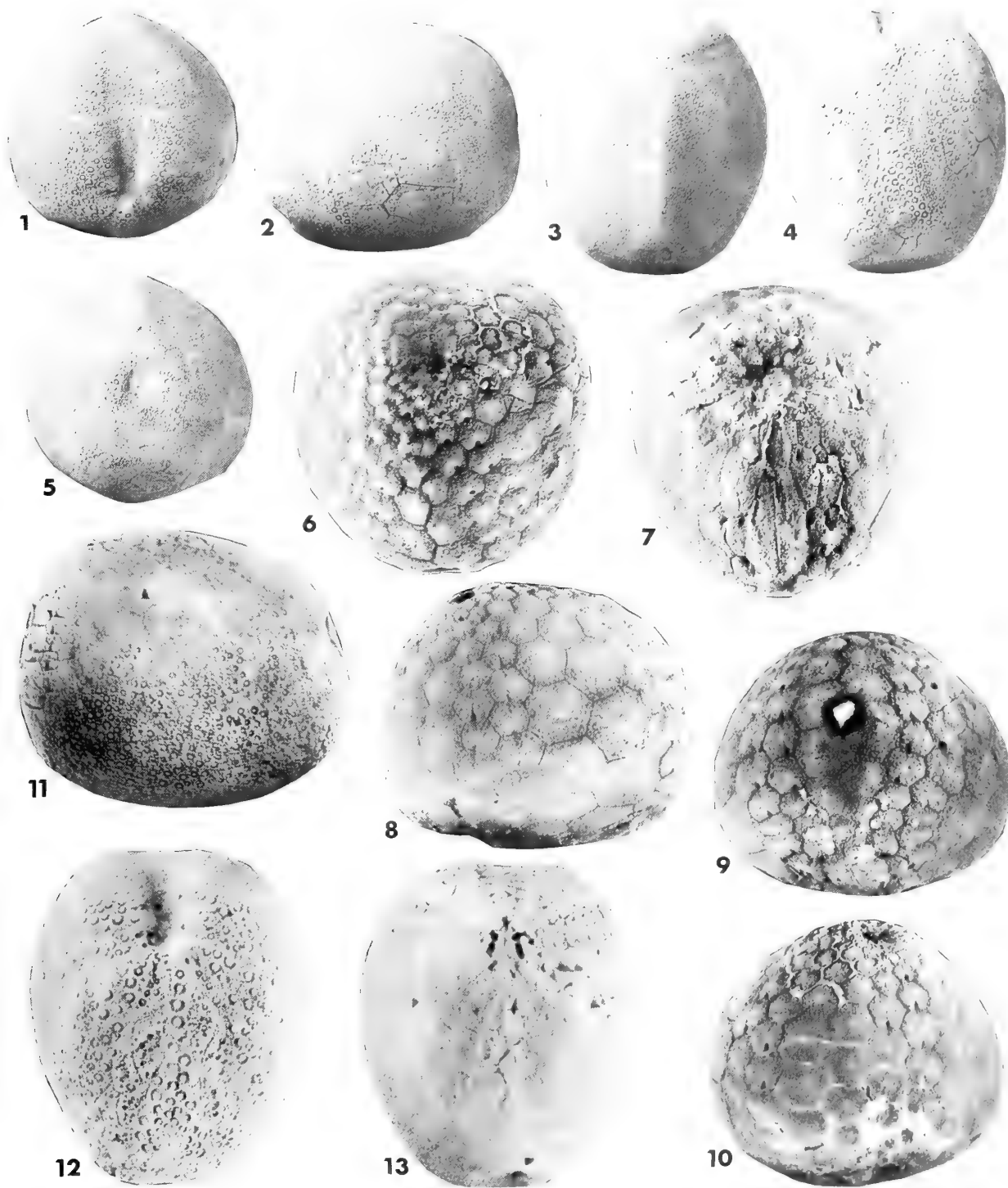
MATERIAL STUDIED. BMNH EE6211–17, EE6226–32, MGB 37307–18, 37325–39, 37365.

PLATE 10

Figs 1–5 *Coraster beneharnicus* Seunes, 1888, BMNH EE4823; Thanetian of Larumbe, Navarra. Anterior, lateral, apical, oral and posterior views, $\times 1.5$.

Figs 6–10 *Ovulaster reticulatus* sp. nov., BMNH EE6074 (**holotype**), Maastrichtian of Sarasate, Navarra. Apical, oral, lateral, posterior and anterior views, $\times 2$.

Figs 11–13 *Coraster beneharnicus* Seunes, 1888, BMNH EE6221; Thanetian of Larumbe, Navarra. Lateral, oral and apical views, $\times 2$.



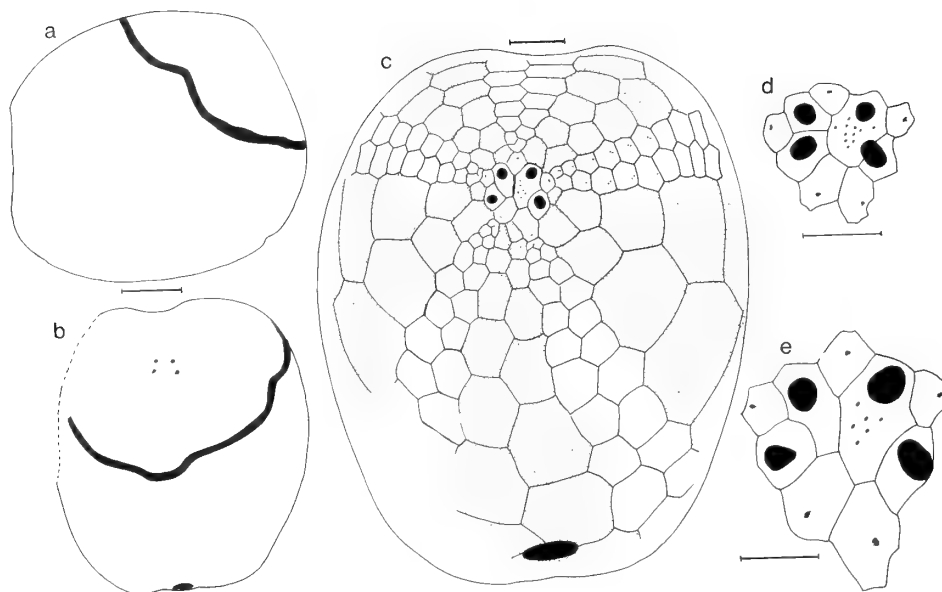


Fig. 36 Camera lucida drawings of plating in *Coraster beneharnicus* Seunes, 1888 from the Danian of Astieso Hill (Sarasate, Navarra); **a, b**, BMNH EE6222, **a**, lateral; **b**, apical surface; **c, e**, BMNH EE6221, **c**, apical surface; **e**, apical disc; **d**, BMNH EE6223, apical disc. Scale bars: **a, b** = 5 mm; **c** = 2 mm; **d, e** = 1 mm.

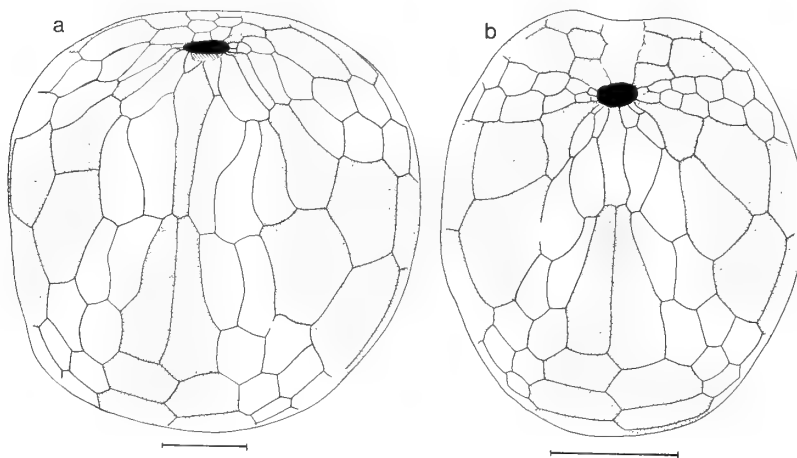


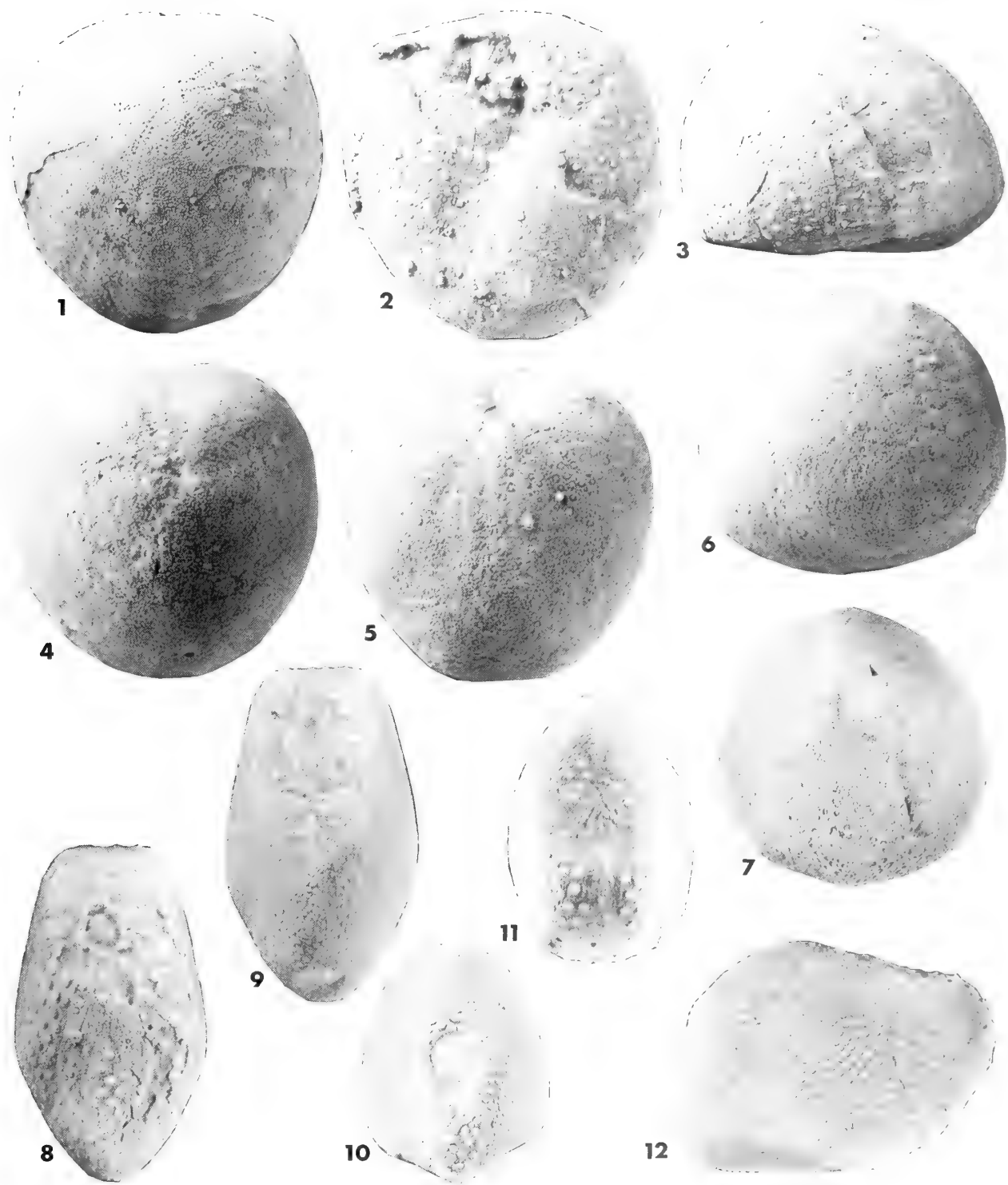
Fig. 37 Camera lucida drawings of plating in *Coraster* species. **a**, *C. vilanovae* Cotteau, 1886; BMNH EE6211 from the early Thanetian of Larumbe (Navarra), oral surface; **b**, *C. beneharnicus* Seunes, 1888; BMNH EE6221 from the Danian of Astieso Hill (Sarasate, Navarra), oral surface. Interambulacra shaded. Scale bars = 5 mm.

PLATE 11

Figs 1–3 *Homoeaster evaristei* (Cotteau, 1886), MGB 37347, Danian of Erice, Navarra. Apical, oral and lateral views, $\times 2$.

Figs 4–7 *Coraster vilanovae* Cotteau, 1886, BMNH EE6212, Danian of Erice, Navarra. Apical, oral, lateral and posterior views, $\times 3$.

Figs 8–12 *Sphenaster larumbensis* sp. nov., BMNH EE6073 (**holotype**), Danian of Larumbe, Navarra. Oral, apical, posterior, anterior and lateral views, $\times 2$.



REMARKS. The position of the peristome varies from being almost at the anterior margin to around 20% of test length from the anterior.

***Coraster beneharnicus* Seunes, 1888**

Pl. 10, figs 1–5, 11–13; Figs 36, 37b

1888a *Coraster beneharnicus* Seunes: 804, pl. 29, fig. 1.

1975 *Coraster beneharnicus* Seunes; Plaziat *et al.*: 635, pl. 1, figs 1–6, text-figs 6, 8.

DIAGNOSIS. Test slightly longer than wide with weak subanal heel. Anterior ambulacrum forming a broad and shallow frontal groove which deepens adorally and extends to the peristome. Peristome up to 25 % of the distance from the anterior.

OCCURRENCE. Danian of Erice, Astieso, Aristregui, Larumbe, Navarra, Spain.

MATERIAL STUDIED. BMNH EE4822–26, EE4842–44EE6070, EE6218, EE6221–25, EE6233; MGB 37345–46, 37354–62, 37368, 37373–78, 37385–401.

Genus **HOMOEASTER** Pomel, 1883

DIAGNOSIS. Test ovate with no frontal groove. Domed to subconical apical surface and flat oral surface. Paired ambulacra non-petaloid to sub-petaloid. Apical system ethmophract and anteriorly positioned, with four gonopores. Peristome small, circular, non-labiate, downward facing. Peripetalous fasciole present, passing just above the periproct posteriorly and at or immediately beneath the ambitus anteriorly.

***Homoeaster evaristei* (Cotteau, 1886)**

Pl. 11, figs 1–3; Fig. 38

1886b *Ornithaster evaristei* Cotteau: 72, pl. 9, figs 5–8.

1892 *Ornithaster evaristei* Cotteau; Nicklés: 115.

1960 *Homoeaster evaristei* (Cotteau); Poslavskaya & Moskvina: 61, fig. 11, pl. 3, fig. 2.

1995 *Ornithaster? evaristei* Cotteau; Gallemí *et al.*: 269, table 1.

1995 *Ornithaster? sp.*; Gallemí *et al.*, table 1.

DIAGNOSIS. Test length up to 30 mm; width approximately 90% of the test length; height 70% of the test length; tallest towards anterior of test. Posterior surface obliquely truncated so that the ovate, longitudinal periproct is just visible from above. Apical system lying 40% of the test length from the anterior margin. Peristome 25% of the test length from the anterior border. Aboral pore-pairs small and slightly circumflexed. Peripetalous fasciole without distinct kink immediately behind the antero-lateral ambulacra.

OCCURRENCE. Danian of Erice, Navarra. The type comes from the Danian of Alfás del Pi, Alicante province, Spain.

MATERIAL STUDIED. BMNH EE6220, EE6235, MGB 37347.

REMARKS. Distinguished from the closely related Upper Cretaceous *H. tunetanus* by its peripetalous fasciole which follows a weakly undulous path around the test. In *H. tunetanus* the peripetalous fasciole is sharply kinked immediately behind the antero-lateral ambulacra.

Genus **OVULASTER** Cotteau, 1884

DIAGNOSIS. Test highly inflated, with anterior sulcus lacking or extremely feeble. Ovate in profile with posterior tapering to a blunt

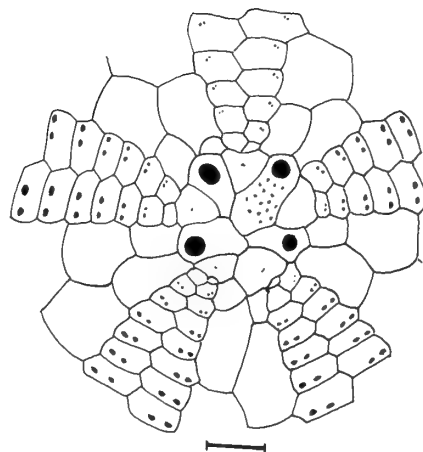


Fig. 38 Camera lucida drawing of plating in *Homoeaster evaristei* (Cotteau, 1886) from the Danian of Erice (Navarra); BMNH EE6220, apical disc. Scale bar = 1 mm.

point. Apical disc ethmophract with four gonopores. Ambulacral plates tall, with small non-petaloid pore-pairs only. Peristome small and circular; slightly depressed. Periproct ovate, placed supra-marginally on steeply sloping posterior part of test. Plastron amphisternous with relatively broad contact between labrum and sternal plates. Subanal fasciole only.

***Ovulaster reticulatus* Smith & Gallemí, sp. nov.**

Pl. 10, figs 6–10; Figs 39, 40

DIAGNOSIS. Ovate *Ovulaster* with ambulacral and interambulacral plates swollen centrally where they are covered in a coarse reticulate stereom meshwork. Aboral tubercles rather coarse and widely scattered. Lower surface of test flatter than in other species. All ambulacra with reduced and obliquely set pore-pairs. Traces of a subanal fasciole are preserved in the paratype, although much of its tuberculation is missing.

TYPES. Holotype BMNH EE6236, paratype BMNH EE6074.

OCCURRENCE. Lower Maastrichtian black shale facies, Sarasate, Navarra, Spain.

REMARKS. The three previously described species of *Ovulaster* all come from the Coniacian-Santonian of North Africa. Compared to *O. reticulatus*, *O. zignoanus* (d'Orbigny) is more wedge-shaped in profile and has a slight frontal sulcus. *O. auberti* Gauthier and *O. obtusus* Cotteau are very rounded in profile and lack the flat base seen in our species. All three North African species lack the distinctive tumid plating with its characteristic reticulate stereom meshwork shown by *O. reticulatus*.

Family **SCHIZASTERIDAE** Lambert in Doncieux, 1905

Genus **LINTHIA** Desor, 1853

DIAGNOSIS. Test cordate with deep anterior sulcus. Paired ambulacra form long, straight, subequal petals. Apical system ethmolytic with four gonopores. Peripetalous fasciole strongly indented between petals. Latero-anal fasciole present. Labral plate relatively short and wide.

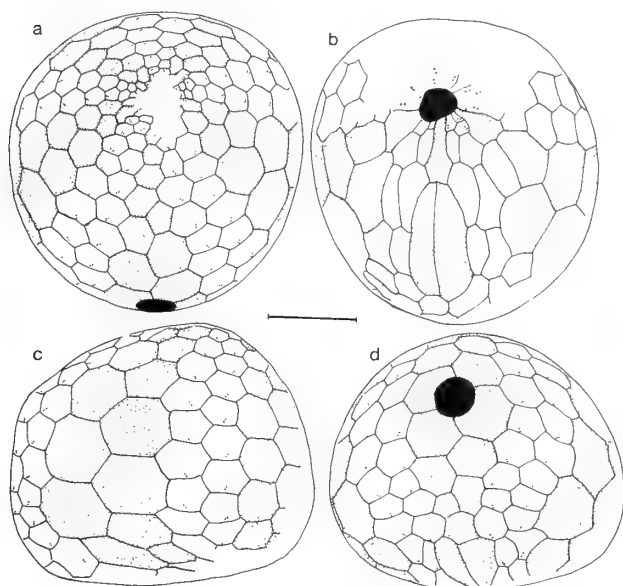


Fig. 39 Camera lucida drawings of plating in *Ovulaster reticulatus* sp. nov. from the Maastrichtian black shale facies at Sarasate (Navarra); holotype BMNH EE6074. **a**, apical surface; **b**, oral surface; **c**, lateral; **d**, posterior. Interambulacra shaded. Scale bar = 5 mm.

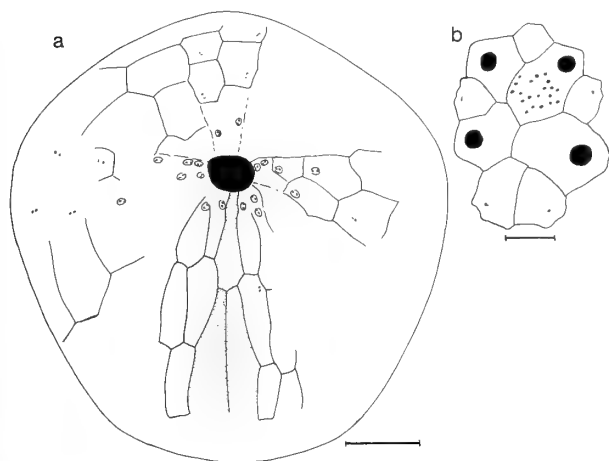


Fig. 40 Camera lucida drawings of plating in *Ovulaster reticulatus* sp. nov. from the Maastrichtian black shale facies at Sarasate, (Navarra); paratype BMNH EE6236. **a**, apical surface; **b**, apical disc. Scale bars: **a** = 5 mm; **b** = 1 mm.

?*Linthia* sp. Fig. 41

OCCURRENCE. Upper Thanetian, *P. pseudomenardii* Zone. Casas de Oraien, Navarra Province, Spain.

MATERIAL STUDIED. MGB 37436.

REMARKS. A single specimen showing the characteristic large plastron and very short, wide labral plate of a *Linthia* (Fig. 41). The upper surface is damaged, but shows a rather wide anterior groove

and the anterior parts of two sunken petals. Impressions in the infilling sediment suggest that the posterior petals were only about half the length of the anterior pair.

Family **AEROPSIDAE** Lambert, 1896

Genus **SPHENASTER** Jeffery, gen. nov.

TYPE SPECIES. *Sphenaster larumbensis* Jeffery, sp. nov.

ETYMOLOGY. From *sphenos* – a wedge.

DIAGNOSIS. Narrow wedge-shaped test. Broad shallowly sunken unpaired ambulacrum with enlarged pore-pairs. Short, flush, non-petaloid paired ambulacra. Ethmophract apical disc with two gonopores. Peripetalous fasciole passes immediately behind the apical system and below the ambitus anteriorly. Enlarged tubercles are developed along the edges of the unpaired ambulacrum.

REMARKS. The new genus is most similar to *Aeropsis*, from which differs in having a wedge-shaped (rather than cylindrical) test with an obliquely truncated posterior, a less anterior apical system and a number of enlarged tubercles on the apical surface. *Aceste* differs in having an ethmolytic apical system, a deeply sunken frontal groove leading to the mouth, single pores in the paired ambulacra and uniform tuberculation. *Sphenaster* is flat across the anterior margin, has pore-pairs in all ambulacra and, although damaged, appears to have no vestibule leading into its mouth.

Sphenaster larumbensis Jeffery, sp. nov.

Pl. 11, figs 8–12; Fig. 42

ETYMOLOGY. Larumbe – the locality at which the specimen was found.

HOLOTYPE. Holotype and only known specimen BMNH EE6073.

OCCURRENCE. Lower Thanetian, upper part of *Coraster* Beds, Larumbe, Navarra Province, Spain.

DESCRIPTION. The holotype measures 14.6 mm in length and 8.4 mm in width (58% of test length). In horizontal outline, the test describes an elongate pentagon. It is flat across the anterior margin, broadens to the widest point (approximately two thirds of test length from the anterior margin) and narrows to the rounded posterior. Maximum height is 10.3 mm (71% of test length), midway along the test. In profile, the test is wedge-shaped, sloping gently to the anterior from the apical system and with a somewhat gibbous lower surface. The posterior is oblique with a very slight subanal heel.

The paired ambulacra are flush and non-petaloid with tiny, inconspicuous pore-pairs. By contrast, the unpaired ambulacrum is broad and slightly sunken and contains enlarged pore-pairs. Pore-pairs are obliquely positioned and diminish in size towards the anterior margin of the test.

The plastron is amphisternous with a long narrow labral plate followed by two equally long, narrow sternal plates. The suture between these plates runs along the midline of the test.

The apical system is positioned 39% of test length from the anterior margin. It has two large genital plates each with a gonopore, and five small ocular plates. A small number of hydropores are present on the madreporite. Plating cannot be clearly made out, but it appears to be ethmophract in structure.

The peristome is circular or rounded pentagonal with no rim. It measures 1.7 mm in diameter (20% of maximum test width) and is situated 21% of test length from the anterior margin. Although the

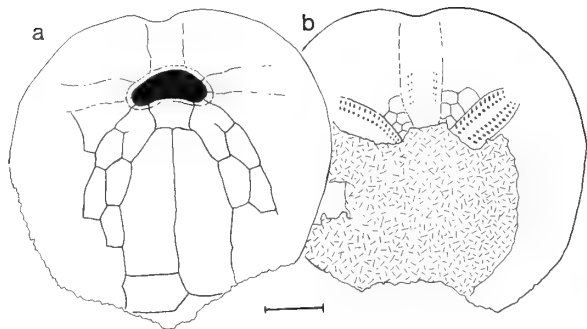


Fig. 41 Camera lucida drawings of plating in *Linthia* sp. from the late Thanetian of Casas de Oraien (Navarra); MGB 37436, a, oral surface; b, apical surface. Scale bar = 5 mm.

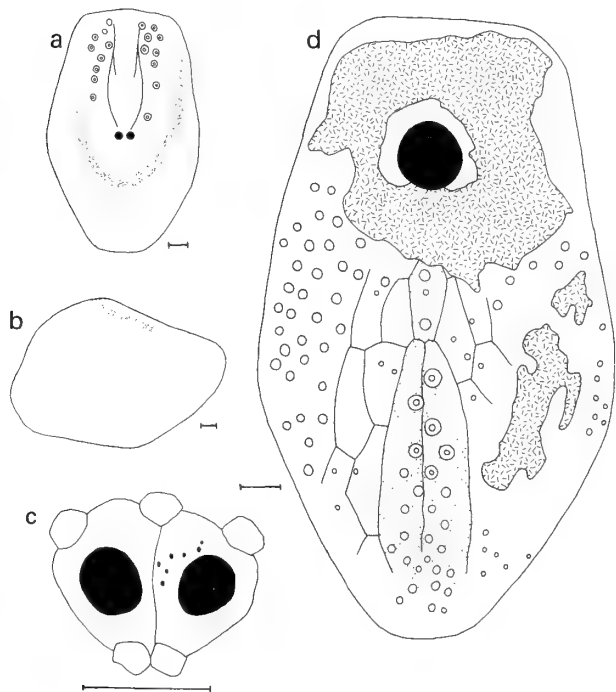


Fig. 42 Camera lucida drawings of plating in *Sphenaster larumbensis* sp. nov., BMNH EE6073 (holotype), from the early Thanetian of Larumbe, Navarra. a, apical surface; b, lateral profile (fasciole stippled); c, apical disc; d, oral surface. Scale bars = 1 mm.

oral surface of the test is damaged, it is clear that the labral plate does not extend over the mouth. The periproct is also circular and measures 2.0 mm in diameter. It is positioned high on the oblique posterior of the test, 52% of test height from the base.

A distinct peripetalous fasciole is positioned high on the test. It passes immediately behind the apical system and crosses the anterior margin at the ambitus. At its broadest point, the fasciole is 8 miliaries wide. The fasciole becomes less distinct towards the anterior where a number of small tubercles are incorporated.

Tubercles are perforate and crenulate and are fairly densely distributed over the aboral surface of the test with scattered miliaries in between. The largest tubercles are positioned on the anterior margin

at the end of the frontal ambulacrum and on the posterior below the periproct. Tubercles are most densely packed around the periproct. Overall, the test has a somewhat granular appearance. On the oral surface, tubercles are far sparser and on the whole larger than on the upper surface. The largest tubercles are situated on the plastron.

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APPENDIX

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Maastrichtian	Distribution	Paleocene	Fate of genus
<i>Tylocidaris (Sardocidaris) trempina</i>	San, Tre		?Pyrenees	survivor
<i>Tylocidaris (Sardocidaris) ramondi</i>	Nav			
<i>T. (Oedematocidaris) baltica</i>	Dmk, NGer			
<i>T. (Tylocidaris) inexpectata</i>	San, Lim			survivor
<i>T. (Tylocidaris) hemmoorensis</i>	NGer			
<i>Goniocidaris</i> sp. A	Lim			survivor
<i>Phyllacanthus regalis</i>	Lim			survivor
<i>Temnocidaris magnifica</i>	San, Fr			
<i>Temnocidaris danica</i>	Lim		Dmk, Lim	survivor
<i>Temnocidaris nigellensis</i>	Belg Dmk, Eng, NGer		Dmk	
<i>Stereocidaris herthae</i>	Dmk, NGer, Eng, Pol			
<i>Stereocidaris pistillum</i>	NGer, Eng		Dmk	survivor
<i>Stereocidaris</i> sp. A	NGer		Dmk	
<i>Stereocidaris</i> sp. B	Dmk			
<i>Almucidaris falgarseensis</i>	Tre			victim
<i>Cidaris rosenkrantzi</i>	Lim		Lim, Dmk	survivor
<i>Cidaris bolli</i>	Dmk			
<i>Echinothuria</i> sp.	NGer, Lim, Dmk		Dmk	survivor
<i>Centrostephanus</i> sp.	NGer, Lim, Dmk		Lim, Dmk	survivor
<i>Orthopsis miliaris</i>	Lim, Tre, San			
<i>Hyposalenia heliophora</i>	n/p		Lim, Dmk	immigrant
<i>Salenia desori</i>	NGer			
<i>Salenia belgica</i>	Dmk, Belg		Belg, Lim	survivor
<i>Salenia sigillata</i>	Lim, Eng			
<i>Salenia geometrica</i>	Lim, Tre			
<i>Pleurosalenia heberti</i>	Eng			survivor
<i>Pleurosalenia anthophora</i>	NGer, Dmk, Lim, Fr, Belg, Pol			
<i>Pleurosalenia maastrichtensis</i>	Lim, Belg, Nav			
<i>Pleurosalenia pygmaea</i>	NGer, Dmk			
<i>Salenocidaris garumnensis</i>	Pyr			
<i>Salenocidaris gallemi</i>	Alic			
<i>Goniopygus tetrachyma</i>	Pyr, San, Tre			
<i>Goniopygus minor</i>	Lim		Lim, Fr, Belg	survivor
<i>Codiopsis disculus</i>	Tre, Lim		Fr	survivor
<i>Phymosoma hexaporum</i>	Tre, Sant			
<i>Phymosoma granulolum</i>	Dmk, NGer, Belg, San, Fr		Dmk, Lim	survivor
<i>Phymosoma koenigi</i>	NGer			
<i>Diplotagma vanderhami</i>	Lim			victim
<i>Diplotagma</i> sp.	San			
<i>Gauthieria alternans</i>	Dmk, NGer			survivor
' <i>Gauthieria</i> ' <i>maeandrinum</i>	Lim			
<i>Gauthieria pseudoradiata</i>	Lim, Dmk, NGer, Belg			
<i>Gauthieria middletoni</i>	Dmk, NGer			
<i>Gauthiosoma princeps</i>	Eng, Dmk, NGer, Lim			
<i>Gauthiosoma krimica</i>	Belg, Dmk		Pol	survivor
<i>Acanthechinus savigni</i>	Pyr			
<i>Acanthechinus</i> sp.	San			survivor
<i>Micropsis batalleri</i>	Tre			survivor
<i>Trochalosoma taeniatum</i>	Dmk, NGer, Lim, Tre, Belg			emigrant
<i>Trochalosoma rutoti</i>	Lim			
<i>Phymotaxis tournoueri</i>	Lim		Pyr	survivor
<i>Circopeltis</i>	n/p		Lim	immigrant
<i>Micropsidia salis</i>	Lim		Lim	survivor
<i>Winkleria maastrichtensis</i>	Lim			victim
<i>Zeuglopleurus werhlii</i>	NGer, Eng			victim
<i>Thylechinus vanderhami</i>	n/p		Lim	immigrant
<i>Coenholectypus nachtigali</i>	Tre, San, Alic			victim
<i>Coenholectypus macrostomus</i>	Lim			
<i>Camerogalerus cantabrigius</i>	San			victim
<i>Conulus magnificus</i>	Dmk, NGer			victim
<i>Conulus gigas</i>	Pyr, Tre, San			
<i>Globator darderi</i>	Alic			victim
<i>Adelopneustes boehmi</i>	NGer		Dmk, Lim, Belg	survivor
<i>Galerites vulgaris</i>	Eng, NGer, Alic			victim

APPENDIX Cont.

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Distribution		Fate of genus
	Maastrichtian	Paleocene	
<i>Galerites stadensis</i>	Dmk, Lim, NGer		
<i>Galerites sulcatoradiatus</i>	Eng, Lim, Dmk, Belg		
<i>Galerites? dollfusi</i>	Rug, Fr		
<i>Echinogalerus belgicus</i>	Lim, Belg		victim
<i>?Echinogalerus vetschauensis</i>	Lim, San		
<i>Echinogalerus muelleri</i>	Lim, San, Nav, Tre		
<i>Echinogalerus? minutus</i>	Lim		
<i>Plagiochasma cruciferum</i>	Lim	Lim, Dmk, Belg	survivor
<i>Catopygus fenestratus</i>	Lim		victim
<i>Hemicara pomeranum</i>	NGer, Pol		victim
<i>Zuffardia</i> sp.	San		emigrant
<i>Faujasia apicalis</i>	Lim		victim
<i>Oolopygus pyriformis</i>	Lim, Alic, San, Fr		survivor
<i>Hardouinia (Fauraster) priscus</i>	Tre		victim
<i>Rhynchopygus marmini</i>	Lim, Fr, ?San		victim
<i>Procassidulus lapiscancrini</i>	Lim		survivor
<i>Stigmatopygus bervillei</i>	n/p	Fr	immigrant
<i>Rhyncholampas macari</i>	Lim, San		emigrant
<i>?Gitolampas scrobiculatus</i>	Lim, Sant, Nav		survivor
<i>Neocatopygus arnaudi</i>	n/p	Pyr	immigrant
<i>Nucleopygus coravium</i>	Lim, Belg, San, Nav		emigrant
<i>Nucleopygus carezi</i>	Pyr		
<i>Clypeolampas ovatus</i>	Fr, San, Alic		victim
<i>Oriolampas michelini</i>	n/p	Pyr	immigrant
<i>Galeaster bertrandi</i>	San, Bas	Dmk	survivor
<i>Garummaster</i>	n/p	Pyr	immigrant
<i>Stegaster altus</i>	Bas, Pyr, Alic, Nav		
<i>Stegaster bouillei</i>	Pyr, Alic, Bas, Nav		
<i>Stegaster coteaui</i>	Pyr, Bas		
<i>Stegaster heberti</i>	Bas		
<i>Stegaster paleocenicus</i>	Nav		survivor
<i>Tholaster munieri</i>	Bas		victim
<i>Pseudoffaster caucasicus</i>	San, Tre		victim
<i>Echinocorys scutata</i>	Lim, Dmk, Pyr, San, NGer Nav, Alic, Belg, Pol	Alic, Pyr Dmk, Nav	survivor
<i>Offaster pilula</i>	Tre, NGer		victim
<i>Offaster leymeriei</i>	Tre, San, Nav		
<i>Jeronia pyrenaica</i>	n/p	Nav, Pyr,	immigrant
<i>Cardiaster granulosis</i>	Lim, Fr, Tre, NGer, Dmk, Belg		
<i>Cardiaster</i> sp.	Pyr	Nav	survivor
<i>Cardiotaxis heberti</i>	Belg, NGer, Dmk		victim
<i>Hagenowia elongata</i>	Dmk, NGer		victim
<i>Pseudholaster faxensis</i>	n/p	Dmk	immigrant
<i>Hemipneustes striatoradiatus</i>	Lim, Pyr, Nav, Alic		
<i>Hemipneustes pyrenaicus</i>	Pyr, Nav, Tre, San, Alic		victim
<i>Hemipneustes oculatus</i>	Lim		
<i>Hemipneustes</i> sp.	Tre, San		
<i>Micraster schroederi</i>	Lim, Belg, Alic		
<i>Micraster aturicus</i>	Alic		
<i>Micraster grimmensis</i>	NGer	?Dmk	survivor
<i>Mokotibaster nicklesi</i>	n/p	Alic	immigrant
<i>Pseudogibbaster tercensis</i>	n/p	Alic, Nav, Pyr	immigrant
<i>Diplodetus duponti</i>	Lim		
<i>Diplodetus maastrichtensis</i>	Lim		
<i>Diplodetus parvistella</i>	Lim		
<i>Diplodetus coloniae</i>	Alic	Pyr, Belg	survivor
<i>Cyclaster grindrei</i>	San, Pyr	Pyr	survivor
<i>Ovulaster granulosa</i>	Nav		victim?
<i>Cyclaster heberti</i>	Alic		
<i>Cyclaster integer</i>	Pyr	Pyr, Dmk	survivor
<i>Cyclaster platumnatus</i>	Rug, Lim		
<i>Cyclaster ruegensis</i>	Rug		
<i>Isaster aquitanicus</i>	Alic	Nav	survivor
<i>Eupatagus mortenseni</i>	n/p	Pyr	immigrant

APPENDIX Cont.

Maastrichtian species recorded from the Maastrichtian and Palaeocene of Western Europe (data from Smith & Jeffery, in press)

Species	Distribution		Fate of genus
	Maastrichtian	Paleocene	
<i>Hemiaster prunella</i>	Fr, Lim, San, Tre, Nav	Dmk	survivor
<i>Hemiaster koninckanus</i>	Lim, San, Nav		
<i>Hemiaster nucula</i>	Fr		
<i>Hemiaster stella</i>	Lim	Dmk, Pyr	
<i>Leymeriaster maastrichtensis</i>	Lim		victim?
<i>Leymeriaster eluvialis</i>	Lim		
<i>Linthia houzeau</i>	n/p	Belg, Fr	immigrant
<i>Paraster</i>	n/p	Lim, Pyr, Dmk	immigrant
<i>Proraster atavus</i>	Tre	Dmk	survivor
<i>Mauritanaster</i> sp. nov.	n/p	Dmk	immigrant
<i>Coraster vilanovae</i>	Alic	Pyr	survivor
<i>Homoeaster tunetanus</i>	Alic	Alic	survivor
<i>Sphenaster larumbe</i>	n/p	Nav	immigrant

KEY TO LOCALITIES

Alic = Alicante
 Bas = Basque region (Zumaia-Bidart)
 Belg = Cipro Dmk = Denmark basin
 Eng = Norfolk, England
 Ger = Pomerania (northern German mainland)
 Lim = Limburg (Maastricht region)
 Nav = Navarra
 n/p = not present
 Pol = Poland
 Pyr = French Pyrenees (Haute-Garonne)
 Rug = Isle of Rügen
 San = Santander
 Tre = Tremp

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